Revision of ammonoid biostratigraphy in the Frasnian (Upper Devonian) of the Southern Timan (Northeast Russian Platform)

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ABSTRACT:

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New field work in outcrops of the Ukhta Region (Southern Timan) together with the re-exanimation of former collections allows a detailed revision of the ammonoid zonation in one of the classical Frasnian regions of Russia. There is a total of 47 species, 18 of which are new or recorded for the first time from the region. The latter applies to representatives of *Linguatornoceras*, *Phoenixites*, *Aulatornoceras* s.str. and *Acanthoclymenia*. New taxa are *Chutoceras manticoides* n.gen. n.sp. and *Linguatornoceras yudinae* n.sp. In the Ust'yarega Formation regional *Hoeninghausia nalivkini*, *Timanites keyserlingi* and *Komioceras stuckenbergi* Zones can be recognized which correlate with the international Frasnian divisions UD I-B/C. The *Ponticeras domanicense* Zone (UD I-E) occupies most of the Lower Domanik, the *Nordiceras timanicum* Zone (UD I-F to I-H) is developed in the Middle and Upper Domanik. Following a poorly defined and short interval with rare *Carinoceras*, pelagic sequences of the Lyaiol Formation (Members 2-4) fall in the *Virginoceras ljaschenkoae* and *Manticoceras lyaiolense* Zones (UD I-I/J). Late Frasnian deposits (UD I-K/L) have not yielded any ammonoids so far. Correlation between the new zonation and the conodont zonation (Montagne Noire zones) is provided.

Key words: Timan, Russia, Devonian, Frasnian, Ammonoids, Goniatites, Biostratigraphy.

INTRODUCTION

The Devonian rocks of the Timan-Pechora region (Text-fig. 1) have become famous since the first reports on his expedition by KEYSERLING (1844,

1846) who described amongst his fossils a range of new goniatites from the Ukhta region. Since a later monograph (HOLZAPFEL 1899), the area has been recognized as one of particular importance for international Devonian ammonoid biostratigraphy. Material collected by HOLZAPFEL found its way to museums outside Russia (e.g., Berlin). MILLER & WARREN (1936) recognized the homonymy of *Goniatites acutus* KEYSERLING with *G. acutus* MÜNSTER and re-named the type-species of *Timanites* as *Ti. keyserlingi*. LYASCHENKO (1956, 1957, 1973) and LYASCHENKO & *al.* (1969) added significant new information on ammonoid faunas and described several new species. Four regional zones defined by the appearance of *Koenenites nalivkini, Timanites acutus, Gephyroceras domanicense* and *Manticoceras intumescens* were recognized (Text-fig. 4). All faunas were revised and monographed by BOGOSLOVSKIY (1969) in a study which not only included classical material but which provided for the first time section descriptions, particularly from the Usa River Basin, and from along the Chut, Ukhta and Vezhavozh Rivers. However, no attempt was made to update the existing or to develop an independent Timan ammonoid succession; faunas were assigned to classical Frasnian zones of Germany. KUSHNAREVA & *al.* (1978) tried to establish a detailed lithostratigraphical subdivision of the Domanik Formation and distinguished successive goniatite and conodont levels within their lithological units. In recent years some revision has been attempted (YATSKOV & KUZ'MIN 1992, MENNER & *al.* 1992, YATSKOV 1994, KUZ'MIN & YATSKOV 1997) which is superceded by data presented here. Detailed descriptions of sections with



Fig. 1. Map of the north-eastern part of European Russia showing the Timan Range and Pechora Basin with the studied region around Ukhta (see frame) in the southern part of the Devonian outcrop (in black)

precise occurrences of old and new goniatite collections were given in a Field Guide to the excursion of the International Subcommission on Devonian Stratigraphy in 1994 (YUDINA & MOSKALENKO 1994, 1997). Included were, however, some rather enigmatic records, including invalid and non-existing taxa as Manticoceras complanatum, such "Aulotornoceras drevermanni" and Tornoceras simplex. Furthermore, a few anomalous occurrences based on vague taxonomy (e.g., Uchtites from the Lyaiol Formation, Virginoceras from the Upper Domanik Formation) should be ignored since they could not be confirmed subsequently by continuing field work or by examination of all available collections.

The following revision of the Southern Timan ammonoid zonation was conducted in 1994 to 1998 within INTAS Project 93-750 on "Mid-Palaeozoic greenhouse anoxic and eustatic events in the Timan, Urals and western European regions". Results are based on a restudy of BOGOSLOVSKIY's material (by MRH & RTB), a study of new material (mostly collected by S. YATSKOV, formerly PIN; other material by VVM) and collections made in 1994 (by MRH & RTB). The position of ammonoid localities is marked in Text-fig. 2. Text-fig. 3 shows the correlation of regional chronostratigraphic units, lithostratigraphy, ammonoid and conodont zones; a summary range chart of all goniatite taxa is given in Text-fig. 4. Despite the long research history and



Fig. 2. Location of outcrops and ammonoid localities in the vicinity of the Ukhta, Lyaiol and Vezhavozh Rivers and their position in relation to lithostratigraphical units

despite the admirable efforts of HOLZAPFEL (1899) and BOGOSLOVSKIY (1969), the number of species is here increased by a further eighteen forms, some of which are completely new, some of which are new to the Timan and to all of Russia, and some of which are only recognized in open nomenclature. This leaves the prospect that even more intensive collecting could bring to light more rare taxa, especially if more efforts are put into cm-by-cm collecting since rare forms tend to be restricted to narrow faunal bands with peculiar paleoecological conditions.

Interest in the goniatite faunas of the southern Timan is heightened by the occurrence of forms originally considered (see HOLZAPFEL 1899) endemics although some have since been reported elsewhere. These include Timanoceras (BOGOSLO-VSKIY 1957), Uchtites (BOGOSLOVSKIY 1958) (also reported from China - Kong & al. 1985), Domanikoceras (BECKER & HOUSE 1993) and Komioceras (BOGOSLOVSKIY 1958) although the last has since been recognized in the Urals and Novava Zemlya (CHOCHIA & ADRIANOVA 1952, YATSKOV 1994). Nordiceras (BOGOSLOVSKIY 1955) has not only been reported from the Timan but also from the Kolyma region of Eastern Siberia (NALIVKIN 1936). The spectacular oxyconic genus Timanites was considered an endemic until it was recognized in Western Canada (MILLER & WARREN 1936) and then in Australia (GLENISTER 1958, BECKER & al. 1993) and there are records from other Russian regions south- and northwards along the Ural seaway. Reports of Timanites in Germany and North Africa refer to homoeomorphic members of the Eobeloceratidae (BECKER & HOUSE 1993). Another curious feature of the goniatite faunas is the dominance of ponticeratids in levels significantly younger than those where it is commonest in other areas (Germany, Morocco). Noteworthy absenties from the Southern Timan area are the Frasnian Triainoceratidae and Beloceratidae. There is also an interesting lack of some gephuroceratid genera such as Serramanticoceras, Costamanticoceras, Maternoceras and Trimanticoceras whilst there are abundant representatives of the M. latisellatum Group with a wide and rather symmetric flank saddle. The result is to give to the Southern Timan goniatite faunas a very distinctive stamp and to raise some questions as to their correlation with successions elsewhere, especially with the new zonation for the Frasnian established in Western Australia (BECKER & al. 1993, BECKER & HOUSE 1997) and New York (HOUSE & KIRCHGASSER 1993).

Abbreviations of ammonoid genera:

Lb. = Lobobactrites, D. = Domanikoceras, L. = Linguatornoceras, Lo. = Lobotornoceras, Au. = Aulatornoceras, Ph. = Phoenixites, Tr. = Truyolsoceras, H. = Hoeninghausia, Ti. = Timanites, Ko. = Komioceras, M. = Manticoceras, C. = Carinoceras, V. = Virginoceras, P. = Ponticeras, Ac. = Acanthoclymenia, U. = Uchtites, N. = Nordiceras. Abbreviations of conodont genera: Pa. = Palmatolepis, Po. = Polygnathus, Ad. = Ancyrodella, Ag. = Ancyrognathus, Me. = Mesotaxis, Pl. = Playfordia.

Deposition of material: Specimens with MB.C.-numbers are stored in the Museum für Naturkunde, Berlin. PIN-numbers refer to the Paleontological Institute of the Academy of Science, Moscow, which also holds the large collections of unnumbered specimens listed in the appendix.

REGIONAL AMMONOID ZONATION OF THE SOUTHERN TIMAN

Ammonoid faunas are treated in a simple lithostratigraphical frame, which is summarized in Textfig. 3. Taxa are briefly commented when they enter; species which needed detailed revision are described in the systematic chapter. Zones are based on the successive first entry of name-giving zonal markers and, in some cases, of associated species. Few outcrops contain more than one faunal level but the age relationships of outcrops are not only controlled by lithological characteristics and by their ammonoids, but also independently by conodont faunas (see ammonoid-conodont correlation chapter). Most sections have been illustrated in YUDINA & MOSKALENKO (1994, 1997); faunas of BOGOSLOVSKIY (1969, 1971) were revised as far as possible, based on the Moscow collections, but most of his sections were not re-visited. A detailed review of the regional facies history, sequence stratigraphy and sealevel history will be given by HOUSE & al. (in press); a shorter English summary was recently given by Kuz'MIN & YATSKOV (1997).

Hoeninghausia nalivkini Zone

DEFINITION: Entry of *H. nalivkini* or of other species of *Hoeninghausia*.

REMARKS: The oldest goniatites of the Southern Timan were found by LYASHENKO (1956, 1957) at the right bank of the Yarega River near the Vodny

UPPER DEVONIAN AMMONOIDS FROM THE TIMAN, RUSSIA

stage	regional stages	formations		members	old conodont assignments	MN zones	regional assembl.	regional ammonoid zonation	intern. zones	miospore zonation
	LIVNIAN		West Tebuk Reef		Uppermost <i>gigas</i>		XI		ļ-L	G. subsuta
		Ukhta	Vanyu Reef		Upper gigas Lower gigas	13	x	[no fauna]		
	EVLANOVIAN		Sedyu			?			I-K	A. speciosa
				4		12	IX	Manticoceras lyaiolense Virg. ljaschenkoae (Carinoceras sp.)	[-]	
			Lyaiol	3						
N A I	SYRACHOIAN	Syrachoy		2		11			- -	M. radiatus
	VETLASYANIAN	Vetlasyan		1		10			1-н	C. vetlasjanicus
	Domanikian	Domanik		Upper	Ag.	9	VII	(Lobotomoceras strangulatum)		
Z						<u>8</u> 7	- vi -	Nordiceras	I-G	S. bellus
S				Middle	unangularis	6	V	timanicum	I-F	
RA				Lower	Po. timanicus	5	IV	(Pont. auritum) Pont. domanicense	I-E	G. semilucensa
–								Komioceras	<u>- 1-U -</u>	P. donenais
		:		Upper	0-1	4	III 	Tim. keyserlingi	I-C	
	SARGAEVIAN Ust	Ust′ya	arega	Middle	rotundiloba	3	п	Hoen. nalivkini	LR	C. optivus
						1-2				S. krestovnikovii
	TIMANUAN	Timan		Upper		?		[no fauna]	I-A	
G[<	HIVIANIAN			Lower	Ad. binodosa		0			

Fig. 3. Correlation of regional substages, lithostratigraphic units, regional (old: e.g., YUDINA & MOSKALENKO 1994, new: OVNATANOVA & *al*. 1999) and Montagne Noire (KLAPPER & *al*. 1996, HOUSE & *al*. in press) conodont zones, regional (new) goniatite zones, international ammonoid subdivisions (BECKER & *al*. 1993) and of miospore zones (AVCHIMOVITCH & *al*. 1993) in the Southern Timan

Settlement in the middle member of the Ust'yarega Formation. These oxyconic forms were described as Koenenites nalivkini (see also Kuz'MIN & YATSKOV 1997) but have to be placed in Hoeninghausia since Koenenites includes only species with rounded venter. Richer faunas of the nalivkini Zone occur in the Northern Timan, in the Usa River Basin (see BOGOSLOVSKIY 1969) and at Chernyshow Ridge. H. uchtense (LYASHENKO) from the Uz-Ruz-shor and Great Adak Rivers was made by LYASHENKO (1956) the type of Protimanites. Examination of the type confirmed the view of BOGOSLOVSKIY (1969)that Protimanites uchtensis does not develop an extra small umbilical lobe at adult stages, which would justify generic separation; Protimanites therefore falls in synonmy of Hoeninghausia. This requires a new generic assignment of the Australian open umbilicate Hoeninghausia pons GLENISTER, which

was placed by BECKER & al. (1993) in *Protimanites*. New *Hoeninghausia* material including an advanced new species from the Chernov Ridge, Kozhim, Saryuga River and Syvyu River (all Northern Timan/Polar Urals) will be decribed elsewhere. BOGOSLOVKIY (1969, p. 265) noted that *H. uchtensis* occurs in the Southern Timan but this has not been confirmed by material available to us.

The *H. nalivkini* Zone was first recognized by LYASHENKO (1957) as *Koenenites nalivkini* Zone (see also TSZYU 1967, YATSKOV & KUZ'MIN 1992, YUDINA & MOSKALENKO 1994, KUZ'MIN & *al.* 1997; Text-fig. 5). BOGOSLOVSKIY (1969) included the *nalivkini* Zone in his Ia faunas and corrected the generic assignment of the zonal index. KUSHNAREVA & *al.* (1978) recorded *Hoeninghausia* as a subgenus of *Koenenites*. YATSKOV (1994) first used the correct zonal name.

Timanites keyserlingi Zone

DEFINITION: Entry of Ti. keyserlingi.

REMARKS: At a higher level in the middle member of the Ust'yarega Formation, again near Vodny, right bank of the Yarega River, small faunas with *Timanites keyserlingi* MILLER and tornoceratids enter (BOGOSLOVSKIY 1969, p. 38; see also YUDINA & MOSKALENKO 1994, Outcrop 16). Various species of *Tornoceras* and *Linguatornoceras* have been included by BOGOSLOVSKIY in *T. simplex*, a taxon that, however, does not exist since *Goniatites simplex* v. BUCH is a questionable (nomen dubium) open



Fig. 4. Ranges of all ammonoid species in relation to lithostratigraphy, sampled localities and beds, ammonoid and Montagne Noire conodont zones; regionally significant conodont species which seem to allow a finer correlation of ammonoid beds are given in addition

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umbilicate Givetian holzapfeloceratid (see BECKER 1993).

In the lower part of the Upper Ust'yarega Formation there are two *Timanites* beds which crop out in three localities of the Chut River (BOGOSLOVKIY 1969, p. 38; Outcrop 7, YUDINA & MOSKALENKO 1994, p. 22). Specimens from the Timanites beds are rather large-sized reaching 15 cm diameter (see Pl. 1, Figs 7-8). According to BOGOSLOVSKIY the same beds have also abundant Tornoceras (probably T. typum SANDBERGER & SANDBERGER) and, at locality 15v, ?Manticoceras sp. in the upper bed. The latter record resembles the oldest occurrence of manticoceratids in Australia (BECKER & al. 1993). Shale units between and above limestones with goniatites have not yielded fauna. The Timanites Beds are thought to have formed in a deepening interval (Timan Event of BECKER & HOUSE 1997).

The *Ti. keyserlingi* Zone was first recognized by LYASHENKO (1957) under the name *Ti. acutus* Zone (Text-fig. 5). This practice was followed by TSZYU (1967) and later by KUSHNAREVA & *al.* (1978) who, however, extended the upper range of the zone in order to comprise the total range of the genus. Due to the recognition of the subsequent *K. stuckenbergi*

Zone, this practise is not followed here. The corrected species name was acknowledged by YATSKOV & KUZ'MIN (1992), YATSKOV (1994), KUZ'MIN & YATSKOV (1997) and KUZ'MIN & *al.* (1997). BOGOSLOVSKIY assigned the faunal interval to his Ia.

Komioceras stuckenbergi Zone

DEFINITION: Entry of Ko. stuckenbergi.

REMARKS: At the top of the Upper Ust'yarega Formation, an apparently succeeding group of limestones 0.72 m thick, were measured (by RTB and MRH; Text-fig. 6) at an outcrop about 50 m above the new bridge at Chut River (Outcrop 7) and divided into units A to G (corresponding to much of Bed 2 of YUDINA & MOSKALENKO 1994, p. 23; "boundary limestone", sr/dm, of KUSHNAREVA & *al.* 1978); these were followed by green shales measured to 0.48 m. Beds A (0.14 m) and B (0.10 m), referred to as the *Komioceras* Beds, contain *Timanites* n. sp. (Pl. 1, Figs 5-6), *Komioceras stuckenbergi* (HOLZAPFEL), *T. typum* (Pl. 2, Figs 7-8), *Domanikoceras timidum* BECKER & HOUSE (Pl. 2, Figs 1-2), *Manticoceras* sp. and *Lobobactrites*

lithostratig	graphy	this paper	Kuz 'min & Yatskov 1997	Yatskov 1994	Yatskov & Kuz'min 1992 Yudina & Mosk. 1994	Kushnareva & <i>al.</i> 1978	Bogoslovskiy 1969	Lyashenko 1957
	Mbr. 4 Mbr. 3	Manticoceras Iyaiolense					l beta/ gamma	Manticoceras intumescens
LYAIOL FM.	Mbr. 2	Virginoceras Ijaschenkoae	Manticoceras cordatum	Manticoceras cordatum	Manticoceras cordatum	Manticoceras intumescens		
	Mbr. 1	(Carinoceras sp.)						
	Upper	Lobotomoceras strangulatum			Manticoceras			
	Middle	Nordiceras timanicum	Manticoceras ammon		ammon	Manticoceras ammon		
Domanik Fm.	Lower	Ponticeras auritum Ponticeras domanicense	Probeloceras domanicense	[not specified]	Probeloceras domanicense	Ph. (Nord.) timanicum Geph. (Probeloceras) domanicense	l alpha	Probeloceras domanicense
	Upper	Komioceras stuckenbergi	? Komioceras stuckenbergi	Komioceras stuckenbergi	Komioceras stuckenbergi	Timanites		
UST' YAREGA		Timanites keyserlingi	Timanites keyserlingi	Timanites keyserlingi	Timanites keyserlingi	acutus		Timanites acutus
FM.	Middle	Hoeninghausia nalivkini		Hoeninghausia nalivkini	Koenenites nalivkini	Koenenites (Hoeninghausia) nalivkini		Koenenites nalivkini
	Lower							

Fig. 5. Correlation of Timan ammonoid zonations of various previous authors with the new proposed succession

timanicus SCHINDEWOLF. BOGOSLOVSKIY (1969, pp. 39-40) added records of *?Truyolsoceras keyserlingi* (MÜLLER) and mentioned a second locality across from the Chut River mouth. The unusual, large and thick-shelled bivalve *Lunulicardium* is also unique at this level (under study by P. JOHNSTON, Tyrell Museum, Canada).

New collections (see Pl. 1, Fig. 4) give clear evidence that *Manticoceras* was present in late Sargaevian time and this eliminates doubts recently raised by KUZ'MIN & YATSKOV (1997). Available material is too small and poorly preserved to allow currently a definite species identification. The new but somewhat doubtful generic assignment of *Aulatornoceras keyserlingi* (= *Goniatites cinctus* KEYSERLING non MÜNSTER) is based on the lack of ventral flares or spines (see Pl. 2, Fig. 12) which characterize all true *Aulatornoceras* (see BECKER 1993). There are similarities with the Famennian *Truyols. bicostatum* (HALL) but in the Timan species the umbilicus closes very early in ontogeny (Pl. 2, Figs 12-13; see also illustration of specimens in HOLZAPFEL 1899 and BOGOSLOVSKIY 1970) which erroneously may suggest affinities with *Phoenixites* (see generic assignment of *keyserlingi* in KUZ'MIN & *al.* 1997). *Ti.* n.sp. is very similar to *Ti. keyserlingi* but significantly smaller in size (< 5 cm diameter); final taxonomic separation of the two succesive *Timanites* forms in the Upper Ust'yarega Formation, however, requires more statistical investigation. The



Fig. 6. Diagrams illustrating the section along the Chut River (Outcrop 7 of YUDINA & MOSKALENKO 1994) exposing the Upper Ust'yarega and Lower Domanik Formations; numbers refer to conodont samples of A. KUZ'MIN; 1st to 3rd level = 1st to 3rd *Ponticeras* Beds, uy = (upper) Ust'yarega Formation, dm = Domanik Formation, dm₁ = lower member, dm₂ = middle member; for details of goniatite faunas see text and appendix

distinction between early and later *Timanites* was already known to LYASHENKO (1957) who recorded *Ti. acutus* var.

A single specimen from new collections of the *Komioceras* Beds (MB.C.2731.1) has the very involute shell form of *Timanites* but lacks the secondary outer umbilical lobes giving a suture as in *Uchtites*. It sits on one block with a *Timanites* n.sp. (MB.C.2731.2) and indicates that the latter genus, characterized by a more open umbilicus, may have been derived via such intermediate forms by sutural simplification rather than having descended from *Ponticeras*. The specimen under question shows sutures only one side but consistent morphology in fifteen densely spaced successive septa speaks against a pathological feature. Until more material becomes available, an identification as *?Uchtites* n.sp. is given.

Beds C (0.08 m) and D (0.17) above the Komioceras Beds contained abundant T. typum. Beds E (up to 0.06 m), F (0.09 m) and G (0.08 m), of very dark bituminous calcarenites (Text-fig. 6), yielded no goniatites. Green shales marking the base of the Domanik Formation commence with Bed H. The fauna in its basal part is not sufficient to indicate an age. KUSHNAREVA & al. (1978), however, reported the presence of K. stuckenbergi and Manticoceras sp. in the lowest metre of the Domanik (Member Idm) which probably correlates with our Beds I/J (compare Lower Domanik zonal range in YATSKOV & Kuz'MIN 1992). In the light of doubts raised by KUZ'MIN & YATSKOV (1997, p. 31), the range of Komioceras above the Sargaevian need to be confirmed by further detailed sampling in Beds I to L.

Faunas of the *K. stuckenbergi* Zone were included by LYASHENKO (1957) in his *Gephyroceras domanicense* Zone and assigned to Ia by BOGOSLOVSKIY (1969). By contrast, and obviously based on the occurrence of *Timanites*, KUSHNAREVA & *al.* (1978) assigned the *Komioceras* Beds to their *Ti. acutus* Subzone of Ia (Text-fig. 5). The alleged higher (basal Domanik) *Komioceras* level was aligned with their "*Pharciceras-Gephyroceras*" Subzone of Ia. Independence of the *stuckenbergi* Zone was first recognized by YATSKOV & KUZ'MIN (1992).

Ponticeras domanicense Zone

DEFINITION: Entry of *P. domanicense* or, regionally, of other species of *Ponticeras*.

REMARKS: The regional final extinction of members of the Koenenitidae (*Timanites, Komioceras*) and the dominance of Ponticeras in the Lower Domanik Formation gives a very clear cut break ("Domanik Crisis" of Kuz'MIN & al. 1997) which correlates with a global extinction of last koenenitids. The basal Domanik transgression is thought to correlate with the Middlesex Event of BECKER & al. (1993). The P. domanicense Zone is best developed in outcrops along the Chut and Ukhta Rivers. Several ponticeratid species with flattened venter have formerly been included in Probeloceras (BOGOSLOVSKIY 1969; KUZ'MIN & YATSKOV 1997) but none of the established Timan forms has the typical pointed zigzag-like suture of the true Probeloceras (see HOUSE & KIRCHGASSER 1993 and BECKER & al. 1993) or the subtriangularly-shaped flank saddle of Acanthoclymenia. The latter genus, however, is recorded as a very minor faunal element from new collections and this is the first evidence for the presence of this genus in northern Russia. It should be noted that a flat venter is also developed in mature stages of the type species *P. aequabile* (BECKER in prep.).

At Outcrop 7, in Bed N (Text-fig. 6), a dark grey recrystallized limestone about 2 m above the *Komioceras* Beds, and 1.66-1.78 m above the base of Bed H, *T. typum*, *D. timidum* (Pl. 2, Figs 3-4), and *Lobobactrites* sp. occur and in Bed 0, only 10 cm above, the same three forms were found together with *Ponticeras* cf. *tschernyschewi* (HOLZAPFEL).

In the 20 metres overlying the calcarenites of Bed G at Outcrop 7 (Text-fig. 6), there are three faunal levels rich in ponticeratids from which S. YATSKOV (formerly PIN, Moscow) retrieved good new collections. These are labelled as the 1st to 3rd Ponticeras Beds on Text-fig. 4 but conodont sample levels are given in Text-fig. 3. The 1st Level, about 11.8 m above the Domanik base (at Outcrop 7, sample 6), introduces P. domanicense (HOLZAPFEL), P. keyserlingi (HOLZAPFEL), P. uchtense (KEYSERLING) and P. bisulcatum (KEYSERLING). More detailed collecting is required to place precisely the level of entry of Uchtites syrjanicus but BOGOSLOVSKIY (1969) recorded this distinctive species from levels which correlate with the 1st Ponticeras Bed. New collections also include an intermediate between T. typum and L. clausum (Text-fig. 6E; Pl. 2, Figs 9-10) and, from a loose block 400 m downstream from the bridge, T. contractum which is characterized by a lower ventral saddle than in T. typum (Text-fig. 6C; Pl. 2, Figs 5-6).

A large goniatite collected loose (by MRH) from the Lower Domanik Formation at Outcrop 7 shows acute lateral lobes unlike *Ponticeras* but as in *Manticoceras* and it is assigned to *Chutoceras manticoides* n.gen. n.sp. (Text-fig. 8A-B; Pl. 1, Figs 1-2). Since only the 1st *Ponticeras* Bed crops out directly in the upper part of the Chut River cliff, it is inferred that this is the source of the specimen. The same may be true for the poorly known *Mixomanticoceras backlundi* (HOLZAPFEL) which has not been found again for a century.

The 2nd Ponticeras Bed (Outcrop 7, sample 9211, Text-fig. 6), at about 18 m above the base (Text-fig. 4) carries basically the same fauna. From the 3rd Ponticeras Bed, about 20.8 m above the base (Outcrop 7, sample 10), which is mottled light blue, the fauna includes novelties which could serve for a subzonal division. Of special importance are new ponticeratids such as P. regale (HOLZAPFEL), P. auritum (HOLZAPFEL), P. uralicum (HOLZAPFEL) and the first moderately abundant occurrence of Manticoceras such as M. ammon (KEYSERLING) and M. sinuosum (HALL). These may allow the recognition of an upper subzone but *M. ammon* is not recommended as subzonal index because of the taxonomic problems of the rare manticoceratids from lower down (Komioceras Beds and levels in the basal Domanik). TSYGANKO (1994, p. 7), for example, quoted a co-occurrence of *M*. cf. *ammon* and *K*. stuckenbergi. Also, there would be the danger of confusion with the partly/mostly younger *M. ammon* Zone of former authors which is discussed below. It seems wiser to use *P*. auritum or *P*. uralicum as possible subzone marker. Based on its symmetric flank saddle, M. ammon seems to have been the evolutionary starting point for a larger group of younger (Lyaiol Formation) Timan manticoceratids (M. latisellatum Group).

A second loose block 400 m downstream of the bridge (leg. RTB, Pl. 1, Text-fig. 3) yielded a single *Acanthoclymenia* aff. *genundewa* (CLARKE). *?Tr. keyserlingi* is now also recorded by juveniles from conodont residues. BOGOSLOVSKIY (1969, p. 41) described similar assemblages including *Uchtites* from the left and right banks of the Ukhta River. Typical light grey limestones with *Ponticeras* are also known from the Lyaiol River (Outcrop 1351).

The choice of the zonal index goes back to LYASHENKO (1957) who established a regional *Gephyroceras domanicense* Zone that, however, embraced lower (*Komioceras* Beds) and higher (Middle/Upper Domanik) faunas (Text-fig. 5). Without explanation, TSZYU (1967) used *Gephyroceras uchtense* instead as zone fossil for the same interval. In KUSHNAREVA & *al.* (1978), the base of the zone was raised to the base of the Lower

Domanik and they introduced a regional M. ammon Zone in their Domanik members IVdm (starting with the M. ammon bearing 3rd Ponticeras Bed) and Vdm (Middle/Upper Domanik). BOGOSLOVSKIY (1969) included Lower Domanik faunas in Ia and assigned the index species to Probeloceras. Restriction of the domanicense Zone to the present faunal interval commenced with YATSKOV & KUZ'MIN (1992). Despite taxonomic revision by BECKER & HOUSE (1993) and BECKER & al. (1993), outdated placing of *domanicense* the in Probeloceras was kept in YUDINA & MOSKALENKO (1994), KUZ'MIN & YATSKOV (1997) and KUZ'MIN & al. (1997) which is corrected here.

Nordiceras timanicum Zone

DEFINITION: Entry of *N. timanicum*, *Phoenixites* and of *M. lamed* in faunas lacking any *Ponticeras*.

REMARKS: Middle Domanik Formation faunas are best documented from exposures beside the (Outcrop Domanik River 21, Yudina & MOSKALENKO 1994, p.25). Bed 96 comprises lenticular dacryoconarid-rich siliceous limestones with Manticoceras ammon, M. lamed (G. & F. SANDBERGER), and T. typum. Bed 97, immediately above, is also lenticular and also rich in dacryoconarids and especially buchiolinids and it includes Nordiceras timanicum (HOLZAPFEL) (Pl. 3, Fig. 1), T. typum, Linguatornoceras sp., ?Tr. keyserlingi (Pl. 2, Figs 11-14), Ph. frechi (WEDEKIND) (Pl. 3, Figs 5-6), Ph. cf. varicatus (WEDEKIND) (Pl. 3, Figs 7-8), M. lamed (Pl. 3, Figs 4, 15-16), M. ammon (Pl. 3, Figs 2-3) and Lb. ?termierorum (CLAUSEN). The Middle Domanik is easily characterised by the disappearance of the various ponticeratids and by the entry of a new faunal complex including Nordiceras. This genus seems to represent an evolutionary side brach from Ponticeras that developed additional ventral lobes as an iteration to beloceratids which differ by their sigmoidal saddles and acute lobes. The zonal marker, unfortunately, seems to be a relative rare form but it also has been reported from apparently the same level of NE Siberia (NALIVKIN 1936). LYASHENKO (1957) made no zonal distinction between Lower and Middle/Upper Domanik ammonoid assemblages. The regional extinction of ponticeratids, the subsequent dominance of Manticoceras, and the regional first appearance of Phoenixites, however, aid the recognition of the timanicum Zone. The later used regional *M. ammon* Zone of the Timan (KUSHNAREVA & *al.* 1978, YUDINA & MOSKALENKO 1994) is illdefined since the index species has been found much lower in the Domanik Formation (see KUZ'MIN & YATSKOV 1997 and discussion above).

Smaller faunas from the main part of the Middle Domanik Formation with M. ammon, M. lamed, N. timanicum, T. contractum and Ph. varicatus are known from several places along the upper reaches of the Lyaiol River (e.g. Outcrop 1903). In all outcrops, lower and middle members of the Domanik can be distinguished by facies differences; limestones of the middler member are darker and richer in Buchiola. Outcrops 503, 504, near Shudayag on the left bank of the Ukhta River yielded faunas from upper parts of the Middle Domanik Formation. The fauna is essentially the same as lower down; N. timanicum was found together with M. ammon and M. lamed in Outcrop 504b. Kuz'MIN & al. (1997) and KUZ'MIN & YATSKOV (1997) recorded M. drevermanni from the Middle Domanik Formation but elsewhere this is a younger Frasnian species and no specimen with sharply triangular saddle (see holotype suture in BECKER & HOUSE 1994) has so far been observed in the Timan.

The Upper Domanik Formation yielded hardly any fauna from the lower and middle parts but sampling has been insufficient so far. Outcrops along the Ukhta and Lyaiol Rivers produced goniatites from the upper part of the member. The best succession is documented in Lyaiol River Outcrop 1904 (= Outcrop ORLOV-1) and it suggests that Upper Domanik faunas can be distinguished at subzonal level by the entry of the previously poorly understood Lobotornoceras strangulatum (KEYSERLING) (Pl. 3, Figs 9-12, 17). Associated species are the same as in the Middle Domanik: M. ammon, M. lamed, N. timanicum (Pl. 3, Figs 15-16), L. aff. clausum, T. contractum and T. cf. typum. Phoenixites has so far only been recognized together with *M. lamed*, anaptychi and a fragmentary second species of ?Truyolsoceras in the topmost two metre of the upper member in Outcrop 13 (samples 7001/7002) near Shudayag on the Ukhta River.

LYASHENKO (1957) did not separate Middle/Upper Domanik faunas within her *Gephyroceras domanicense* Zone. BOGOSLOVSKIY (1969) made no comments on the stratigraphic position of *Nordiceras* at all since no additional material since HOLZAPFEL (1899) was known to him. This may explain why KUSHNAREVA & al. (1978) erroneously aligned *N. timanicum* with *P. domanicense* as the Lower Domanik marker (Text-fig. 5). Middle/Upper Domanik faunal levels were part of their M. ammon Zone.YATSKOV & KUZ'MIN (1992) raised the base of the *ammon* zone to a level within Domanik Member IVdm, obviously excluding the 3rd Ponticeras Bed at the border between IIIdm and IVdm although it contains M. ammon. This was followed by YUDINA & MOSKALENKO (1994). KUZ'MIN & YATSKOV (1997) discussed the problem of *M*. *ammon* as index species and reported oxyconic Virginoceratinae from the Upper Domanik which otherwise seemed to be very poor in ammonoids. Therefore, the base of their M. cordatum Zone was lowered to the base of the Upper Domanik. The new material of N. timanicum from various levels in the Middle/Upper Domanik Formation not only clarifies its stratigraphic position but allows the establishment of a well-defined new zone which escapes the problems associated with the total range versus acme of M. ammon.

(Carinoceras sp. Interval Zone)

DEFINITION: Disappearance of typical Domanik ammonoid faunas and rare entry of *Carinoceras*.

REMARKS: Near the top of the Domanik formation the typical assemblage of the middle/upper member disappears suddenly and this gives a third important regional ammonoid extinction. Nordiceras. ?Truvolsoceras, Phoenixites and Lobotornoceras probably faced regional extinction due to the termination of their favourite eutrophic and anoxic Domanik facies by basinwide regression. Pelagic sequences of the succeeding Lyaiol Formation were somewhat better oxygenated which allowed the settlement of the seafloor by various brachiopods such as chonetids, Chonetipustula and stratigraphically important rhynchonellids. The gap between rich ammonoid faunas of the Upper Domanik and higher Lyaiol Formations is partly closed by the regional rare first appearance of oxyconic gephuroceratids assigned here to Carinoceras. The Carinoceras sp. occurrences indicate an interval zone (interregnum) with poor faunal representation. Kuz'MIN & YATSKOV (1997) included it in their M. cordatum Zone. The regressive Vetlasyan episode gives not much hope for the finding of richer faunas from this interval. However, it is remarkable that Carinoceras has been found in shallower and more neritic facies in other regions such as the Ardennes, Boulonnais and southern Morocco.

KUZ'MIN & YATSKOV (1997, p. 31) recorded from a carbonate concretion level of the topmost

Domanik of Outcrop 1904 a Virginoceras sp. (leg. A.N. ORLOV, St. Petersburg) which was formerly identified (unpublished reports) as Carinoceras sp. Unfortunately, this specimen was not available for study. Another example of Carinoceras sp. comes from the base of the Syrachoy Formation, from a level equivalent to the sandstone unit right on top of Vetlasyan Formation (see YUDINA the & MOSKALENKO 1994, Text-fig. opposite p. 29). This specimen (last seen in Moscow in May 1995) is very compressed, rather large and resembles C. oxy (CLARKE) auct. Type material of the latter species, however, have fat inner whorls as in the Sphaeromanticoceras rhynchostomum Group and will be transferred to that or to a new genus. Currently, large-sized compressed carinoceratids are without name but taxonomic revision has to await additional material. Carinoceras LYASHENKO (1957) predates and is not a synonym of Carinocera (IREDALE & LASERON 1957) (Caenogastropoda, Caecidae).

Virginoceras ljaschenkoae Zone

DEFINITION: Entry of *V. ljaschenkoae* or of other marker species such as *C. menneri*, *L. yudinae* n.sp., *M. latisellatum*, and *M. solnzevi*.

REMARKS: Ammonoids are lacking from Member 1 of the Lyaiol Formation which is regarded as an equivalent of the shaly Vetlasyan Formation. Beds with ammonoids assigned to Member 2 of the Lyaiol Formation are best documented from the Vezhavozh and Lyaiol Rivers. Since the Lyaiol Formation represents a reduced sequence which is laterally equivalent to various levels in the Vetlasyan, Syrachoy and early Ukhta Formations (Text-fig. 3), careful and very detailed collecting is required for discrimination. This has only recently been commenced with detailed bed numbering of the outcrop sequence.

According to conodonts (see correlation chapter), the oldest Lyaiol goniatite faunas may come from the lower part (Beds 14-19) of Outcrop 1906 at Lyaiol River (Text-fig. 3). These produced a distinctive assemblage with *C. menneri* (LYASHENKO), ?*V. ljaschenkoae* (BOGOSLOVSKIY), *M. carinatum* (BEYRICH), *M. latisellatum* YANISHEWSKY, *M. cordatum* (G. & F. SANDBERGER), *M. solnzevi* (LYASHENKO), *L. clausum* (GLENISTER) and *L. yudinae* n.sp. As a rarity, there is also a single specimen of *Aulatornoceras* cf. *auris* (QUENSTEDT) which represents the first true record of the genus (s.str.) from the Timan and from all of Russia. A second thicker *Aulatornoceras* (MB.C.2759, Pl. 4, Figs 7-8) is assigned to the poorly known *Au. bickense* (WEDEKIND) but unfortunately there is no reliable locality and lithostratigraphy information for the specimen.

Placing of Carinoceras ljaschenkoae in Virginoceras is based on the presence of a secondary saddle in the median ventral lobe as illustrated by BOGOSLOVSKIY (1969, Text-fig. 84). All new specimens show this diagnostic feature. Previously Virginoceras has been placed into synonymy of Neomanticoceras (BECKER & HOUSE 1993, BECKER & al. 1993, YATSKOV 1994) but the latter genus differs by its pointed saddles giving a distinction as between Acanthoclymenia and Probeloceras. Internal moulds have a blunt venter on which the shell builds a hollow and razor-sharp keel. As mentioned above, the M. latisellatum Group is characterized by wide and rather symmetric flank saddles and includes M. regulare FENTON & FENTON of Iowa, M. evolutum PETTER from North Africa and Australia, "P." acutilobatum BOGOSLOVSKIY from the Altai Mts, *M. carinatum* (see sutures of holotype in BECKER & HOUSE 1994), and perhaps also the very thick M. hunanense XU from Southern China. Timanoceras ellipsoidale was probably an offshoot from M. solnzevi. Both M. ammon and M. solnzevi have broad inner whorls which would normally suggest placing in Sphaeromanticoceras (see record of the genus in YATSKOV 1994, p. 48). The latter, however, also has high, narrow and strongly asymmetric flank saddles and well-developed biconvex growth lines. The two rather thick Timan species are, therefore, also assigned to the latisellatum Group which may deserve subgeneric distinction.

Outcrop 8 (YUDINA & MOSKALENKO 1994, p. 36 et seq.) on the right bank of the Vezhavozh River displays a sequence of ammonoid faunas. Unit 3 has been subdivided by RTB and the basal part (Bed 3a) yielded L. clausum, L. yudinae n.sp. (Pl. 4, Figs 1-2, 5-6), M. cordatum, M. latisellatum, M. solnzevi, M. carinatum (Pl. 4, Fig. 12), C. menneri (Pl. 4, Figs 11-12) and Lb. timanicus. V. *ljaschenkoae* is present ca. 60 cm higher (Bed $3h_{11}$) and in Bed 4. Faunas are clearly identical with those from Lyaiol River and generally this applies also to higher beds of Outcrop 1906 and to Vezhavozh outcrops listed by BOGOSLOVSKIY (1969). From Outcrop 16e comes a juvenile specimen (MB.C.2751; Pl. 4, Figs 9-10) of a new species of Acanthoclymenia which is among the youngest records published for the genus. The presence of the rare Ac. forcipifer (G. & F.

SANDBERGER) and *Ac. planorbe* (G. & F. SANDBERGER) in do I γ (now UD I-J) of Germany has not yet been confirmed in modern studies but an even younger species than the new one from the Timan was observed in the *V. erraticum* Zone of the Canning Basin (BECKER & HOUSE in prep.).

Bed 4 at Outcrop 8 as well as faunas of BOGOSLOVSKIY (1969) include large, compressed Manticoceras with narrow and asymmetric lateral saddle. These have been identified as M. intumescens (G. & F. SANDBERGER) but typical specimens of the species are somewhat thicker and have a steeper umbilical wall. Currently a cf. is added to the identification of Timan material. M. buchi (d'ARCHIAC & de VERNEUIL) is more compressed than cf. intumescens. Timanoceras ellipsoidale (= affineformis LYASHENKO) is not present in new collections but was recorded by BOGOSLOVSKIY (1969, Outcrop 16i) from typical Lyaiol 2 assemblages. He also (p. 44) mentioned three M. sinuosum from Outcrop 16i which, unfortunately, were not seen during a revision of his material in Moscow.

Beds 6 and 7 higher in Member 2 of the Lyaiol Formation at Outcrop 8 were recorded by YUDINA & MOSKALENKO (1994, p. 38) to contain a fauna that resembles those from lower down apart from a somewhat reduced diversity. The presence of Timanoceras ellipsoidale has not been confirmed in the field in 1994 and confusion with fat M. solnzevi is possible. Outcrop 9, Bed 1 (YUDINA AND MOSKALENKO 1994, p.39 et seq.) on the left bank of the Vezhavozh River, ca. 1.1 m below the top of Member 2, yielded during recent collecting (RTB 1994) in the basal part of the succession youngest C. menneri and V. ljaschenkoae. In addition there was a very large-sized (C. menneri does not reach 10 cm diameter, see BOGOSLOVSKIY 1969, p. 257) and thin Carinoceras sp. with very flat flanks that resembled the rare older specimens mentioned above.

LYASHENKO (1957) introduced a *M. intumescens* Zone and BOGOSLOVSKIY (1969) assigned faunas from the Lyaiol Formation to I β/γ (see also KUSHNAREVA & *al.* 1978). With respect to taxonomic uncertainties surrounding Timan specimens in relation to German types of *M. intumescens*, it seems better to use a different and easy diagnostic species such as *V. ljaschenkoae* as zonal marker. YATSKOV (1994) and KUZ'MIN & YATSKOV (1997) preferred *M. cordatum* instead of *intumescens* as zone fossil and lowered the zonal base to the lower boundary of the Upper Domanik Formation. Elsewhere in the world (e.g., BECKER & *al.* 1993) *M*. *cordatum* appears much earlier (UD I-E) as in the Timan which restricts its use as regional marker.

Manticoceras lyaiolense Zone

DEFINITION: Regional extinction of *Carinoceras*, *Virginoceras* and *M. solnzevi*, followed by a spread of *M. lyaiolense*.

REMARKS: Higher in Outcrop 9 (YUDINA AND MOSKALENKO 1994, p. 29), rich faunas appear just 12 to 18 cm below the top of Lyaiol Member 2 (Bed 2i). They are dominated by *M. cordatum* and *M.* cf. intumescens but lack oxyconic forms such as Carinoceras and Virginoceras. Many specimens show postmortal crinoidal overgrowths. M. solnzevi, M. latisellatum and M. carinatum are also absent. The regional extinction of oxyconic gephuroceratids and the significant decline of the M. latisellatum Group with wide and rather symmetric lateral saddle is a general distinction between Members 2 and 3/4 and can be used to establish a zonal division. There also seems to be an exclusion of Manticoceras faunas including M. lyaiolense from Vezhavozh and the Lyaiol River with oxyconic forms and, therefore, M. lyaiolense is employed as zonal index. It should be noted that there are single records of the marker species from Member 2 at Outcrop 16zh (BOGOSLOVSKIY 1969, p. 44, together with M. solnzevi), Outcrop 16m (Bed 4, BOGOSLOVSKIY 1969, p. 46) and from Outcrop 8 (Bed 7, YUDINA & MOSKALENKO 1994, p. 38). It is possible that some of these specimens came from higher in the succession or they may belong to M. lamed. M. lvaiolense differs from the former only by a narrower umbilicus and intermediates between both taxa have been recognized in Member 4 (Outcrop 1360). Even if M. lyaiolense s.str. can be shown in the future to range down as rare species into the main part of Member 2, the faunal change described above will be still significant enough to allow discrimation of Member 2 versus Member 3/4 faunas within the Lyaiol Formation. Formerly, faunas of the lyaiolense Zone were included in the regional M. intumescens (LYASHENKO 1957, KUSHNAREVA & al. 1978) and M. cordatum (YATSKOV 1994, KUZ'MIN & YATSKOV 1997) Zones.

The basal part of Member 3 at Vezhavozh River, Outcrop 9 (YUDINA & MOSKALENKO 1994: Bed 3) has a sparse ammonoid fauna but is said to include still *M. carinatum*. *M.* cf. *latisellatum* is found together with *M.* cf. *lyaiolense*, *M. lamed*, *M. cordatum* and *L. clausum* at Lyaiol River, Outcrop 1358 at a level which, according to conodonts (highest range of *Palmatolepis semichatovae*) must be low in Member 3. Several other outcrops along the Vezhavozh River were recorded by BOGOSLOVSKIY (1969) to contain similar assemblages.

Sections along Lyaiol River give an ammonoid sequence through the lower to upper parts of Member 4 of the Lyaiol Formation. None of these contain frequent M. carinatum or M. latisellatum but there are large forms with somewhat converging flanks at small size and flat subdiscoidal shells at maturity. These are here identified as M. aff. cordatum but relationships with M. buchi (somewhat more compressed), M. cordatum (flanks more converging) and M. cf. intumescens (somewhat thicker) should be established by rigorous statistical treatment. The lower part of Member 4 is exposed in Outcrop 1359 where M. lyaiolense, M. aff. cordatum and M. cordatum were found. Outcrop 1360 falls in the middle part of Member 4 and has the same fauna but L. clausum, a single M. cf. carinatum, and intermediates between M. lamed and M. lyaiolense in addition. The youngest Southern Timan goniatites come from ca. 5-6 m below the top of Member 4 at Outcrop 1908 and include M. lamed and, again, L. clausum.

Higher Zones

At present there is no evidence for goniatites from the Sedyu and Ukhta Formations. However, it should be noted that the regional M. ammon – M. latisellatum – M. solnzevi lineage developed subconvex growth lines with only very shallow lateral sinus which might lead to confusion with species of *Crickites*. The two lineages are clearly differentiated by the broad, low and rather symmetric lateral saddle of the Timan forms.

CORRELATION OF TIMAN ZONES WITH THE INTERNATIONAL AMMONOID SUCCESSION

The entry of members of the Koenenitidae defines the international Frasnian division UD I-B (BECKER & *al.* 1993) but from an evolutionary viewpoint it is expected that oxyconic lineage appeared somewhat later than *Koenenites* itself within the interval. The *H. nalivkini* Zone of the Southern Timan shows a typical low diversity assemblage of UD I-B (*Koenenites* Genozone) as it is also known from the Canning Basin.

Hoeninghausia itself ranges into the next division and this may be true for the large-sized German type-species *H. archiaci* (GÜRICH) that has pointed secondary outer umbilical lobes as in *H. uchtensis* and *H. koswensis* BOGOSLOVSKIY from the Northern Timan.

Timanites is the international marker genus for division UD I-C and it is restricted to this zone. Regionally UD I-C can be divided into a lower part (UD I- C_1), represented by the *Ti. keyserlingi* Zone, and into the Komioceras Beds with a Komioceras-Timanites association (UD I-C2, main part of K. stuckenbergi Zone). The rare entry of Manticoceras in UD I-C (BOGOSLOVSKIY 1969, p. 38) resembles conditions in the Canning Basin and in Morocco but the genus has several older species in the Genundewa Limestone (UD I-B) of New York (HOUSE & KIRCHGASSER 1993). The doubtful range of Komioceras into the basal part of the Lower Domanik formation, together with MN Zone 5 conodonts (see next section), leaves the possibility that the upper part of the regional stuckenbergi Zone correlatives with division UD I-D which is characterized in New York and Missouri by the entry of Sandbergeroceras.

The P. domanicense Zone is a regional equivalent of UD I-E (Probeloceras Genozone). Apart from conodont correlation, this is corroborated by the entry of advanced Ponticeras in UD I-E of the Canning Basin (BECKER & al. 1993) and by the presence of M. sinuosum in the 3rd Ponticeras Bed of the Timan which enters in New York in the lower Cashaqua Shale (I-E, HOUSE & KIRCHGASSER 1993). The type level of *Ponticeras* is around the Middle/Upper Devonian boundary and the younger Timan group with wider flank saddles may have to be separated. Mixomanticoceras backlundi probably comes from the same stratigraphic level (UD I-E₁) as Mixomanticoceras exploratum (BECKER & al. 1993) from Australia. The international marker of UD I-E, Probeloceras s.str., is absent in the Timan but this is no surprise since all Beloceratidae are absent on the Russian Platform, L. aff, clausum from the 1st *Ponticeras* Bed is the oldest member of the genus; slightly younger undescribed material comes from UD I-F (Prochorites Genozone) and I-G (Mesobeloceras Genozone) of the Canning Basin.

Goniatite assemblages from the *Nordiceras timanicum* Zone have such a strong regional signature that comparison with faunas from elsewhere is difficult. Contemporaneity with UD I-F to the lower part of I-H (*Beloceras* Genozone) is based on conodonts only. *Nordiceras* is an endemic genus of northern Russia and both *M. lamed* and *Ph. frechi* enter in Morocco in Domanik-like black limestones as early as UD I-C. *L. strangulatum* is also endemic and the three described other members of the genus are either older (*L. hassoni* HOUSE, *L.* aff. *hassoni* of HOUSE & KIRCHGASSER 1993) or younger (*L. ausavense* (STEININGER) from Büdesheim, Germany, UD I-I/J). The subsequent *Carinoceras* sp. interval zone correlates with the upper part of UD I-H but, again, this is based on conodont ages. In Australia, Belgium and perhaps even in New York, *Carinoceras* enters much earlier in UD I-F (BECKER & HOUSE 1993, pp. 119-120).

The V. ljaschenkoae Zone includes a range of taxa such as M. carinatum and relatives of M. intumescens that are elsewhere typical for rather high levels in the Frasnian. Placing of Lyaiol Formation faunas into the classical do $I\beta/\gamma$ by BOGOSLOVSKIY (1969) is fully justified by the lack of typical upper Frasnian taxa such as Crickites or Archoceras. In the Canning Basin, Virginoceras enters in the higher part of UD I-J (Neomanticoceras Genozone; regional V. erraticum Zone, BECKER & al. 1993) but conodonts suggest that the Russian species of the genus is older and UD I-I (Playfordites Genozone) in age. Au. cf. auris appears together *Playfordites* tripartitus with (G. & F. SANDBERGER), the I-I zonal marker, in the higher Rhinestreet Shale of New York (HOUSE & KIRCHGASSER 1993) but becomes more common (Germany, Australia, southern France) in UD I-J. The entry of L. clausum low in Member 2 of the Lyaiol Formation fits the appearance of the same species at the base of I-I in its NW Australian typeregion.

The extinction of compressed oxyconic gephuroceratids (= Virginoceratinae) at the base of the M. lyaiolense Zone is a regional feature; the zonal boundary seems to fall within a high level of UD I-I. Faunas from Member 3 and 4 of the Lyaiol Formation do not contain any of the markers of UD I-J such as Neomanticoceras, Clauseniceras (= "Crickites" expectatus Group), Trimanticoceras or advanced Maternoceras. Involute gephuroceratids such as M. lyaiolense seem to have a wider distribution than previously known but Moroccan relatives are from younger Kellwasser Limestone (UD I-K/L, Archoceras and Crickites Genozones). Correlation of the M. lyaiolense Zone with the higher part of UD I-I and with I-J relies on conodont data and on the lack of typical upper Frasnian goniatites as outlined above.

CORRELATION OF TIMAN AMMONOID AND CONODONT ZONES

Until rather recent years (KUSHNAREVA & al. 1978, Ovnatanova & Kononova 1984, Yatskov & Kuz'min 1992, Yudina & Moskalenko 1994; see Text-fig. 1) Timan conodont successions have been assigned to a mixture of old Frasnian zones of ZIEGLER (1962, 1971) and of regional zones (e.g., Polygnathus timanicus Zone). Based on borehole material, KLAPPER & al. (1996) successfully applied the thirteen-fold Montagne Noire zonation (MN zones) to the Frasnian of the Timan-Pechora region which is followed here but completed by numerous additional outcrop data (KLAPPER, KUZ'MIN & OVNATANOVA in HOUSE & al. in prep., superceding KUZ'MIN & al. 1998). In parallel there have been attempts to establish an alternative regional zonation (KUZ'MIN & YATSKOV 1997, KUZ'MIN 1997) and a succession of eleven regional assemblages, named as O to XI (Text-fig. 5), has recently been introduced by OVANATOVA & al. (1999). In addition, certain species of Palmatolepis, Mesotaxis, Ancyrognathus and Ancyrodella are rather important for the finer distinction of ammonoid levels within zones and formations (see Text-fig. 4). It has not been possible so far, to apply the so-called Frasnian standard zonation of Ziegler & Sandberg (1990).

The oldest Southern Timan ammonoids of the *H. nalivkini* Zone enter in the Middle Ust'yarega Formation later than *Ad. africana* (first occurrence at the top of the lower member). Originally (KLAPPER 1989, p. 453) this species was supposed to appear in the upper part of MN 3 but more recently (KLAPPER 1997) its composite range in graphic correlation (up from 99.1 CSU) was not listed to stretch below that of *Pa. transitans*, the index of MN 4 (from 99.0 CSU). In Timan outcrops *Ad. africana* enters always below *Pa. transitans* and whilst its composite range should be re-considered, correlation of the *H. nalivkini* Zone within the MN3/4 transition is left open. So far, there is no overlap between *H. nalivkini* and *Pa. transitans*.

The *Ti. keyserlingi* Zone falls in the lower part of MN 4 but *Pa. transitans* was only found in the Upper *Timanites* Bed (KUZ'MIN & YATSKOV 1997, p. 34, sample 9102). The *Komioceras* Beds also fall in MN 4 but have a distinctive fauna with *Me. bogoslovskiy* and *Pl. primitiva* that enables the discrimination in the Southern Timan of an upper part of the zone (KUZ'MIN & YATSKOV 1997, Text-fig. 4; compare KLAPPER & *al.* 1996, p. 133). The base of the Lower Domanik is dated as basal part of MN 5 giving a rather young age for the possible upper range of *Komioceras* which, however, needs to be re-confirmed.

The new oldest level with Ponticeras at Chut River (Beds N/O) also falls in the basal part of MN 5 and correlates with a level slightly above oldest Pa. maximovae and Pa. keyserlingi. The 1st Ponticeras Bed has Pa. gutta as a characteristic faunal element that allows the regional recognition of a middle part of MN 5. Near the top of the Lower Domanik, in the 3rd Ponticeras Bed, Ad. curvata early form has been found suggesting a very high position in MN 5 (see composite range in KLAPPER 1997). Faunas of the N. timanicum Zone from the Middle Domanik are associated with Pa. bohemica, Pa. spinata, Pa. domanicensis s.str. and Ozarkodina trepta which clearly indicate MN 6. The level with L. strangulatum in the upper part of the Upper Domanik yielded Pa. cf. luscarensis and Pa. proversa which are indicative of MN 9-10 (see composite ranges in KLAPPER 1997). Therefore, there is currently a gap in the ammonoid record that spans all of MN 7 and 8. MN 10 is well developed in the Upper Domanik of Outcrop 1904, somewhat above the goniatite faunas.

The two levels with rare Carinoceras at the top of the Upper Domanik and at the base of the Syrachoy Formation have not been precisely dated with conodonts but an assignment to MN 10 is without doubt because of MN 10 faunas below and because of the entry of MN 11 faunas higher in the sequence. The regional Carinoceras sp. interval zone obviously does not represent much time. The V. ljaschenkoae Zone falls into MN 11 with Pa. semichatovae as the important index conodont associated with most faunas. In the lower part of Outcrop 1906, Pa. semichatovae is not present but Pa. elegantula and relatives of Pa. timanensis instead which may indicate MN 11. Higher levels within the zone at Outcrops 8 and 9 have Pa. aff. winchelli which seems characteristic for a higher level within MN 11 (see composite range in KLAPPER 1997).

The base of the *M. lyaiolense* Zone still falls in the top part of MN 11 with *Pa. semichatovae* but *M. lyaiolense* is not frequent below the base of MN 12 (e.g., Outcrop 1358). Faunas from Member 4 of the Lyaiol Formation have species such as *Pa. gyrata*, *Pa. orlovi*, *Ag.* aff. *altus* and *Ag. amana* that enter in a higher position within MN 12. No ammonoids of MN 13 have been found so far in the Timan.

SYSTEMATIC PALAEONTOLOGY (RTB & MRH)

Family Acanthoclymeniidae

Chutoceras BECKER & HOUSE n. gen.

TYPE SPECIES: *Chutoceras manticoides* BECKER & HOUSE n. sp.

DIAGNOSIS: Large, laterally strongly compressed with flat flanks, subevolute with a narrowly-rounded venter; concavo-convex growth lines with a deep, tongue-shaped ventral sinus, a narrow, rounded and highly projecting ventro-lateral salient, a broad and widely rounded lateral sinus and a indistinctive low salient at the umbilical seam. Suture with a trifid ventral lobe, the lateral of which is very sharp and slightly curved dorsad, with a large semicircular, slightly asymmetric lateral saddle, and with an acute lateral lobe on the inner flank of the adult conch.

REMARKS: The new genus combines the typical strongly compressed and flat shell outline and growth lines of forms usually referred to Ponticeras with outer sutures as in Manticoceras, especially as in the M. latisellatum Group. The dorsal sutures have so far not been observed but there is probably a pointed umbilical lobe. Chutoceras is thought to have evolved iteratively from advanced Ponticeras with sub-evolute shell form and with wide flank saddles by a sharpening of the lateral lobes late in ontogeny. Contemporaneous representatives of Manticoceras are more involute and show a less compressed, well-rounded whorl section and low and broad ventro-lateral and dorso-lateral salients of growth lines. Within the Gephuroceratidae, similar high ventro-lateral salients are only developed in Mixomanticoceras (see BECKER & al. 1993) with tubby, inflated shells and, much later, in similar thick Trimanticoceras (see BECKER & HOUSE 1993).

INCLUDED SPECIES: There are no other described species included in the genus but it occurs in eastern North America (HOUSE & KIRCHGASSER in prep.). Possibly included may be the form from the early Frasnian of Western Australia determined as *M*. aff. *evolutum* in BECKER & *al*. (1993). The evolute *P*. *?acutilobatum* BOGOSLOVSKIY appears to be a relative of the younger, middle Frasnian, *M. evolutum* and belongs to the *M. latisellatum* Group.

Chutoceras manticoides BECKER & HOUSE n. sp. (Text-fig. 8A-B; Pl. 1, Figs 1-2)

TYPE SPECIMEN: Holotype MB.C 2165, Text-fig. 8A-B.

TYPE HORIZON: Lower Domanik Formation, *P. domanicense* Zone.

TYPE LOCALITY: Chut River, Outcrop 7, Ukhta Region, Timan.

DIAGNOSIS: As for genus.

DESCRIPTION: Holotype preserved in light grey styliolitic limestone with the phragmopcone mostly recrystalised. Estimated maximum diameter 120 mm. At the last septum at 93 mm diameter, whorl width is 16.5 mm, whorl height 35 mm and umbilical width 22 mm. Whorl section flat on the lower flanks, converging gently to a narrow, rounded venter; umbilical shoulders short, steep and rounded. Fine growth lines (Text-fig. 7A) show a deep, tongue-shaped ventral sinus, a narrow, rounded and projecting ventro-lateral salient and very broad lateral sinus with an umbilical salient probably centred on the seam. Suture with a trifid ventral lobe, on holotype slightly excentric (Text-fig. 7B), the lateral of which is very sharp and slightly curved dorsad, with a large semicircular, slightly asymmetric, lateral saddle, and with an acute lateral lobe on the inner flank of adult stages. Dorsally, a pointed umbilical lobe is probably present. At a whole whorl from the last septum (at ca. 35-40 mm dm), the lateral lobe has a still rounded narrow base.

COMPARISON: There are two similar umbilicate (around 25% dm) species of *Ponticeras*. *P. regale* reaches similar large size but does not develop pointed lateral lobes and displays ventrolateral furrows and a characteristic concave umbilical wall. *P. uchtense* is obviously smaller, develops a rather flat ("tectiform") venter at maturity, possesses weak dorsolateral ribs and a less developed flank saddle.



Fig. 7. Sutures and growth lines of some Timan Tornoceratidae (Part 1). A. Mature growth lines of *Domanikoceras timidum* BECKER & HOUSE, at 61.2 mm diameter (scale = 5 mm), Chut River, loose block at Outcrop 7, OUM; B. Suture of a juvenile specimen of *Domanikoceras timidum* BECKER & HOUSE, MB.C.2110, at 5 mm whorl height, Outcrop 7, Bed

N; C. Suture of *Tornoceras contractum* GLENISTER, MB.C.2120, at 14.5 mm whorl height, Outcrop 7, 3rd *Ponticeras* Bed; D. Suture of *Linguatornoceras* aff. *clausum* (GLENISTER), MB.C.2115, at 10 mm whorl height, Outcrop 7, 1st *Ponticeras* Bed; E. Suture of *Linguatornoceras clausum* (GLENISTER), MB.C.2160, at 10 mm whorl height, Sedyu River, Outcrop 1360, Lyaiol Formation, Member 4

Acanthoclymenia aff. genundewa (CLARKE 1898) (Text-fig. 8D; Pl. 1, Fig. 3)

- +aff. 1898 Gephyroceras ? (Probeloceras?) genundewa CLARKE, 86.
- aff. 1975 Probeloceras genundewa CLARKE 1898; KIRCHGASSER, pp. 77-82, Text-figs 7B, 8B, 9A-F; Pl. 2, Figs 1-6; Pl. 3, Figs 3, 4, 12-13 [further synonymy].
- aff. 1993 Acanthoclymenia genundewa (CLARKE 1898); BECKER & HOUSE, p. 117.

DESCRIPTION AND REMARKS: The single specimen from Chut River (MB.C.2137) is incomplete due to strong recrystallisation of the phragmocone.



Fig. 8. Sutures and growth lines of some Timan Gephurocerataceae. A. Growth line of the holotype of *Chutoceras manticoides* BECKER & HOUSE n.gen. n.sp., MB.C.2165, at 81 mm diameter, loose block along Chut River, Outcrop 7, probably from the 1st *Ponticeras* Bed;
B. Last suture of the holotype of *Chutoceras manticoides* n.gen. n.sp., at 83 mm diameter (scale = 5 mm); C. Suture of *Nordiceras timanicum* (HOLZAPFEL), MB.C.2763.1, at ca. 8.5 mm diameter, Outcrop 1904, Bed 12; D. Suture of *Acanthoclymenia* aff. *genundewa* (CLARKE), MB.C.2137, at 13 mm diameter, Chut River, 400 m downstream from bridge

At 17.5 mm the umbilical width is ca. 6 mm (34.3%), the whorl height is 6.5 mm (37.1%). The flanks are gently rounded, the venter is flat and rounded but not tabulate.

Ac. genundewa from the Genundewa Limestone of New York has similar shell parameters but is known only from smaller specimens which show stronger flattening of the venter. Tabulate venters, sometimes also ventrolateral furrows, characterize all described other members of the genus. The Timan form probably represents a new species but the only specimen is not well enough preserved for becoming a type.

A juvenile Acanthoclymenia (MB.C. 2751; Text-fig. 10A; Pl. 4, Figs 9-10) from Outcrop 16e of BOGOSLOVSKIY (1969) resembles aff. genundewa in lacking any sign of furrows and ventral flattening but is more evolute and somewhat more compressed. The specimen has 2.9 mm umbilical width (41.4%), 2 mm whorl widths (28.6%), 2.5 mm whorl height (35.7%) and ca. 2 mm apertural height (31.4%) at 7 mm diameter. Growth lines are fine and concavoconvex. The flank saddle forms a wide triangle, the lateral lobe is deep and rounded. The specimen obviously represents a second new species but formal erection should await more and perhaps larger material. Generally, Acanthoclymenia is a much smaller genus than the ancestral Ponticeras which suggests a paedomorphic trend of evolution within the family. The latter applies also to the origin of the micromorphic Gogoceras.

Family uncertain

Nordiceras timanicum (HOLZAPFEL 1899) (Text-fig. 8C; Table 1; Pl. 3, Figs 1, 13-14)

- + 1899 Prolecanites timanicus HOLZAPFEL, 47-48, Pl. 2, Fig. 6
 - 1969 Nordiceras timanicum (HOLZAPFEL 1899); BOGOSLOVSKIY, 286-287, Text-Fig. 96e, Pl. XXVI, Fig. 2 [further synonymy]

DESCRIPTION AND REMARKS: The new material shows most of the shell features described by HOLZAPFEL (1899) but is more evolute (see Table 1). All specimens have more than four whorls at 12-13 mm diameter and are extremely compressed. MB.C.2139 has concavo-convex growth lines with a high ventrolateral salient well preserved. Ribbing is not yet developed and fine parallel concave rugae of the wrinkle layer are visible where the shell has split

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specimen	dm	wh	ah	ww	uw	wh/dm	ah/dm	ww/dm	uw/dm
MB.C.2761	13	5	4.3		4.9	38.5	33		37.7
MB.C.2763.1	12.3	4.8		2	4.5	39		16.3	36.6
MB.C.2139	12	4.9	4		4.4	40.8	33.3		36.7

Table 1. Shell parameter in *Nordiceras timanicum*. [dm = diameter, wh = whorl height, ah = apertural height, ww = whorl width; all in mm, ratios in %]

off. As emphasized by HOLZAPFEL (p. 48), coarse recrystallisation has destroyed all septa and sutures are only visible at the border between transparent blocky calcite of the phragmocone and the body chamber filled by grey micrite. Sutures fully confirm the illustration by HOLZAPFEL (1899, Pl. 2, Fig. 6a) and disprove the different drawing in BOGOSLOVSKIY (1969, Text-Fig. 96e). The best suture is preserved in MB.C.2763.1; all saddles and lobes are narrow and rounded. On the mid-flank there is a deep, lingulate second ventral lobe followed ventrolaterally by a small third ventral lobe. Dorsolaterally, there is a lingulate lateral lobe and a smaller outer umbilical lobe. The presence of another small umbilical lobe at the seam, as indicated by HOLZAPFEL, cannot be decided due to insufficient preservation. A whorl fragment from Outcrop 1907, sample 7 (= Bed 12) indicates a very shallow second lobe at the seam, but dorsally only a narrow dorsal lobe is present. This gives the following sutural formula: $IU_2U_1LE_2E_3E_1$. As mentioned above, Nordiceras does not fit into the Beloceratidae with sigmoidal sutural elements and differs from Acanthoclymeniidae by the appearance of third ventral lobes.

Family Tornoceratidae

Subfamily Tornoceratinae

Linguatornoceras yudinae BECKER n.sp. (Text-fig. 9B; Table 2; Pl. 4, Figs 1-6)

? 1957 Tornoceras cf. cinctum LYASHENKO, p. 194.

TYPE SPECIMEN: Holotype MB.C.2164 (Textfigs 9B-C; Pl. 4, Figs 3-4), a somewhat incomplete specimen best showing constrictions, shell form, growth lines and sutures.

TYPE HORIZON AND LOCALITY: ?Lyaiol River, Lyaiol Formation, Member 2, *V. ljaschenkoae* Zone.

OTHER MATERIAL: Paratypes MB.C.2147, 2750/1-2, 2752, 2760.

DIAGNOSIS: Adult stages compressed and with rounded venter; regularly spaced ventral mould constrictions weaken and disappear during ontogeny; growth lines strongly biconvex with narrow, tongueshaped ventrolateral salient which sits in shallow ventrolateral grooves, lateral sinus wide; sutures with narrowly rounded, deep, slightly asymmetric adventitious flank lobes.

DESCRIPTION: Earliest ontogenetic stages up to 2 mm diameter (MB.C.2750/1) have a very small open umbilicus (ca. 0.4 mm) and inflated whorls; adventitious lobes are still lacking. Later stages have closed umbilici and become compressed with gently curved flanks. Mould constrictions are marked on median stages and are regularly spaced. They appear as insertions with sharp adoral and adapical borders. MB.C.2147 has eight constrictions on the last half, the holotype eleven constrictions on the last whorl. From ca. 20 mm dm on, they become gradually weaker and disappear eventually completely (MB.C.2752). Individually there seems to be varia-

specimen	dm	wh	ah	ww	wh/dm	mh/dm	ww/dm
MB.C.2752	30.6	17.6		13.8	57.5		45.1
MB.C.2164	29	16.7	9.6	12.3	57.6	33.1	42.4
MB.C.2147	22.5	13		99.7	57.8		43.1
MB.C.2760	13.7	8	4.8	ca. 7	58.4	35	ca. 51
MB.C.2750.1	3.3	1.6	1	2.3	48.5	30.3	69.7

Table 2. Shell parameter of Linguatornoceras. yudinae n.sp. [abbreviations as in Tab. 1]



Fig. 9. Sutures of some Timan Tornoceratidae (Part 2). A. Suture of an adult Domanikoceras timidum BECKER & HOUSE, MB.C.2748, leg. HOLZAPFEL, at 14 mm whorl height, probably from Chut River, Komioceras Bed; B. Suture and growth lines of the holotype of Linguatornoceras yudinae BECKER & HOUSE n.sp., MB.C.2164, at 11.3 mm whorl height, probably from Lyaiol River, Lyaiol Formation, Member 2; C. Suture of Lobotornoceras strangulatum (KEYSERLING), MB.C.2753.3, at 4.5 mm diameter, Outcrop 1904, Bed 3 (Upper Domanik); D. Suture of Lobotornoceras strangulatum (KEYSERLING), MB.C.2753.2, at 4 mm whorl height, Outcrop 1904, Bed 3; E. Suture of Phoenixites cf. varicatus (WEDEKIND), MB.C.2758, at 5.5 mm whorl height, Outcrop 21, Bed 97; F. Course of a constriction of Aulatornoceras bickense (WEDEKIND), MB.C.2759, at 4 mm whorl height, locality unclear, probably from

Member 2 of the Lyaiol Formation



Fig. 10. Sutures of Timan Acanthoclymeniidae: A. Acanthoclymenia n.sp. juv., MB.C.2751, at 4.8 mm diameter, BOGOSLOVSKIY Lok. 16e, Lyaiol Formation, Member 2; B. ?Uchtites n.sp., MB.C.2731, at 14 mm whorl height, Outcrop 7, Komioceras Beds (leg. RTB)

tion concerning their strength and ontogenetical change. Ventrolateral furrows with high and tonguelike projecting growth line salient are present in all specimens apart from the juvenile MB.C.2750.1. The largest specimen, MB.C.2752, shows that the low dorsolateral salient becomes wider at maturity. The holotype and MB.C.2147 display a high and well-rounded dorsolateral saddle, deep, lingulate, slightly asymmetric A-lobes and a ventral saddle that is as high as the inner flank saddle. Ventral lobes are small. In MB.C.2752 the A-lobe is slightly wider as in the others.

REMARKS: LYASHENKO (1957) listed a *T. cf. cinctum* from the Lyaiol Formation. Since *?Tr. keyserlingi* (= *Goniatites cinctus Keyserling* non MÜNSTER) does not occur above the Domanik Formation, it is suggested that LYASHENKO saw material of the new species which shares the ventrolateral grooves.

Among Frasnian members of the genus, the new species is related to the widespread *L. clausum* but differs in its constrictions, ventrolateral grooves and by the narrow growth line salient on the outer flanks. *L. linguum* from Germany has more flattened flanks, a rather symmetric flank lobe and also lacks constrictions. The poorly known *L. nummularium* (ROEMER) is more compressed; *L. restrictum* (EICHWALD) has lateral constrictions. Famennian species of the *L. haugi* (FRECH) Group all have hook-like A-lobes.

specimen	dm	wh	ah	ww	uw	wh/dm	ah/dm	ww/dm	uw/dm
MB.C.2753.1	18.3	10.6		ca. 4	0	57.9		ca. 22	0
MB.C.2753.2	8.7	5.3	ca. 3		0	60.9	ca. 34		0
MB.C.2753.2	7	4		2.7	0	57.1		38.6	0
MB.C.2766.1	6.5	3.8		2.5	0.6	58.5		38.5	9.2
MB.C.2753.3	5.2	2.8	1.6	2.3	0.5	53.8	30.8	44.2	9.6
MB.C.2766.2	4.1	2.2	1.4	1.9	0.7	53.7	34.1	46.3	17.1

Table 3. Shell parameter of *Lobotornoceras strangulatum* [abbreviations as in Table 1; it should be noted that all specimens are internal moulds which give larger uw figures than shell material]

The new species is also somewhat reminiscent of the involute *Aulatornoceras eifliense* Group which, however, possesses a ventral band with flares or spines. Both *Aulatornoceras* and *Truyolsoceras* are normally open umbilicate but *?Tr. keyserlingi* resembles *L. yudinae* n.sp. in the complete closure of the umbilicus. The adventitious lobe of the new species and the constrictions are rather typical for *Linguatornoceras* but relationships with *keyserlingi* cannot be ruled out completely.

- Lobotornoceras strangulatum (KEYSERLING 1844) (Text-fig. 9C-D; Table 3; Pl. 3, Figs 9-12, 17)
- + 1844 Goniatites strangulatus KEYSERLING, 228, Pl. A, Fig. 4.
 - 1969 *Tornoceras ? strangulatum* (KEYSERLING 1844); BOGOSLOVSKIY, 58 [further synonymy].

DESCRIPTION: KEYSERLING (1844) gave a rather good description and illustration of the species but whorls expand more rapidly than originally shown. Characteristic are the uniformly strongly compressed shell shape and constrictions throughout ontogeny; these features allow easy identification even of the smallest specimens and of fragments. For this reason, L. strangulatum is a useful marker form. Up to 6-7 mm diameter, the umbilicus is slightly open on internal moulds but it is closed at median and adult stages. There are three prorsiradiate and subconvex constrictions per whorl which are deepest on the venter and which weaken towards the short and rounded umbilical wall. Only in MB.C.2753.2, a slight lateral sinus is indicated. Growth lines are not preserved in the new material. Sutures in MB.C.2753.2 resemble the figure given by KEYSERLING (1944, Pl. A, Fig. 4b) but the lateral lobe sits outside the umbilical seam and is obviously slightly divided. In the juvenile MB.C.2753.3, parts of the last septal face are preserved which show an expansion of the L-lobe but there is not yet a low saddle at the seam.

COMPARISON: The new material allows for the first time a modern understanding of KEYSERLING's species which was not refigured by BOGOSLOVSKIY (1969). Shell form and constrictions are very similar in *L. strangulatum* and *L. ausavense* but the latter species has symmetric, subtriangular flank saddles and deeper, again more symmetric A-lobes. In terms of morphology, suture and stratigraphical range, the Timan species is ancestral to *ausavense* from Büdesheim (Germany). Older species of the genus from North America (*L. hassoni*) and Morocco (*L.* n.sp.) lack constrictions.

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APPENDIX: Frasnian ammonoid record of the Southern Timan

Old goniatite identifications are given in brackets.

1. Hoeninghausia nalivkini Zone (upper UD I-B)

Faunal level 1b: Middle Ust'yarega Formation, main part

Yarega River, right bank, near Vodny, Outcrop 16-K (Outcrop D in Text-fig. 2), Bed 4 (LYASHENKO 1956, 1957, YATSKOV & KUZ'MIN 1992); upper MN 3 to lower MN 4 (with Ad. africana, without Pa. transitans) H. nalivkini

Yarega Town, Oil Pit, leg. Tszyu H. cf. nalivkini juv. (PIN 183-1)

2. Timanites keyserlingi Zone (lower UD I-C)

Faunal level 2a: Middle Ust'yarega Formation, upper part

Yarega River, right bank, near Vodny, Outcrop16 (Outcrop E in Text-fig. 2; BOGOSLOVSKIY 1969: Outcrop 15a), top Bed 2 (see YUDINA & MOSKALENKO 1994, 1997); upper MN 3 to lower MN 4 (with *Ad. africana*, without *Pa. transitans*) *Ti. keyserlingi ?T. typum* Gp. (det. *T. simplex*)

Faunal level 2b: Upper Ust'yarega Formation, lower part, 1st *Timanites* Beds

Chut River, Outcrop 2 (in Text-fig. 2) = BOGOSLOVSKIY (1969): Outcrop 15b, Bed 1 *Ti. keyserlingi*

Chut River, Outcrop 3 (in Text-fig. 2) = BOGOSLOVSKIY 1969: Outcrop 15v, Bed 1 ?*T. typum* Gp. (det. *T. simplex*)

Faunal level 2c: Upper Ust'yarega Formation, lower part, 2nd *Timanites* Bed

Chut River, Outcrop 2 (in Text-fig. 2) = BOGOSLOVSKIY (1969): Outcrop 15b, Bed 3 *Ti. keyserlingi ?T. typum* Gp. (det. *T. simplex*)

Chut River, Outcrop 3 (in Text-fig. 2) = BOGOSLOVSKIY (1969): Outcrop 15v, Bed 3 *Ti. keyserlingi ?T. typum* Gp. (det. *T. simplex*) *?Manticoceras* sp. Chut River, Outcrop 7, Bed 1 (see YUDINA & MOSKALENKO, 1994, 1997) = BOGOSLOVSKIY (1969): Outcrop 15g; sample K9102: lower MN 4 (with *Pa. transitans*) *Ti. keyserlingi*

3. Komioceras stuckenbergi Zone (upper UD I-C to UD-D)

Faunal level 3a: Upper Ust'yarega Formation, *Komioceras* Beds

Chut River, Outcrop 7, Beds A-B (BOGOSLOVSKIY 1969: Outcrop 15g, Bed 3); upper MN 4 (with *Ad. pramosica, Pa. transitans, Me. bogoslovskiy, Pl. primitiva*) *Ti.* n.sp. (det. *Ti. keyserlingi*) (MB.C.2104.1-5, 2732.1-2, Pl. 1, Figs. 5-6) ?Uchtites n.sp. (MB.C.2731.1, Text-fig. 10B) *K. stuckenbergi* (MB.C.2105.1-4, 2747.1-5) *T. typum* (det. *T. simplex*) (MB.C.2106.1-8, Text-fig. 7D, Pl. 2, Figs. 7-8, loose MB.C.2734) ?*Tr. keyserlingi* (see BOGOSLOVSKIY 1969) *D. timidum* (det. *T. simplex*) (loose MB.C.2748, leg. HOLZAPFEL, Text-fig. 9A, Pl. 2, Figs. 1-2) *Manticoceras* sp. (MB.C.2107.1-2, Pl. 1, Fig. 4) *Lb. timanicus* (MB.C.2108)

Chut River, Outcrop 7, Beds C-D (BOGOSLOVSKIY 1969; Outcrop 15g); upper MN 4 *T. typum* (leg. MRH)

Ukhta River, across from Chut River mouth, BOGOSLOVSKIY (1969): Outcrop 15d, Bed 1 *Ti*. n.sp. (det. *Ti. keyserlingi*) *K. stuckenbergi ?T. typum* Gp. (det. *T. simplex*) *?Tr. keyserlingi D. timidum* (according to S. YATSKOV)

Faunal level 3b: Lower Domanik Formation, basalmost part

Chut River, Outcrop 7, basalmost Lower Domanik, ca. 1m above base (LYASHENKO in KUSHNAREVA & al. 1978: Member 1dm; around Bed J); samples 94-96 and D911, 911A-B: lowermost MN 5 (with *Pa. punctata, Me. ovalis, Me. johnsoni*) *Manticoceras* sp. *K. stuckenbergi* ?T. typum Gp. (det. T. simplex)

4. Ponticeras domanicense Zone (UD I-E)

Faunal level 4a: Lower Domanik, basal part

Chut River, Outcrop 7, more than 1.5 m above base of Lower Domanik, Beds N-O; above samples D912 and 97: lower MN 5 (with *Pa. punctata, Pa. maximovae, Me. distinctus*) *P.* cf. *tschernischewi* (MB.C.2113) *D. timidum* (MB.C.2110, Bed N, Text-fig. 7B, Pl. 2, Figs. 3-4; MB.C.2112, Bed O) *T. typum* (MB.C.2109.1-2, Bed N; MB.C.2111, Bed O)

Lobobactrites sp. (MB.C.2738)

Ukhta River, around Chut River mouth (see Outcrop 15e of BOGOSLOVSKIY 1969), ca. 3.5 m above base of Lower Domanik) *Manticoceras* sp. *Tornoceras* sp.

Faunal level 4b: Lower Domanik, 1st Ponticeras Bed

Chut River, Outcrop 7, YUDINA & MOSKALENKO (1994): unit 5 (BOGOSLOVSKIY 1969: Outcrop 15g, Bed 6); middle MN 5 (with Pa. gutta) P. tschernyschewi (MB.C.2117) P. bisulcatum P. uchtense P. keyserlingi (MB.C.2116) P. domanicense Ponticeras sp. indet. (MB.C.2737) Chutoceras manticoides n.gen. n.sp. (MB.C.2165, Text-fig. 8A-B, Pl. 1, Figs. 1-2). U. syrjanicus (see BOGOSLOVSKIY 1969) T. typum (det. T. simplex) (MB.C.2114) L. aff. clausum (MB.C.2115, Text-fig. 7D, Pl. 2, Figs. 9-10) Lobobactrites sp.

(?) Chut River, 400 m downstream from bridge, 1st loose Block (leg. RTB 1994) *P. tschernyschewi* (MB.C.2127.1-2) *P. uchtense* (MB.C.2736.1-2) *P. bisulcatum* (MB.C.2128.1-3) *P. keyserlingi* (MB.C.2129.1-2) *U. syrjanicus* (MB.C.2130) *T. typum* (MB.C.2125.1-3) *T. contractum* (MB.C.2126) *Lb. timanicus* (MB.C.2131)

(?) Ukhta River, left bank, 500 m downstream from Krokhal Creek mouth (see BOGOSLOVSKIY 1969: p. 41), Outcrop 9 *P. bisulcatum P. uchtense P. domanicense*

Chut River, ?Domanik (see HOLZAPFEL 1899) MixoM. backlundi

Faunal level 4c: Lower Domanik, 2nd Ponticeras Bed

Chut River, Outcrop 7 (Member IIIdm in KUSHNAREVA & *al.* 1978); sample D9211: middle to upper MN 5 (with *Pa.gutta*) *P. uchtense P. cf. uchtense P. lebedeffi Ponticeras* sp. *M. ammon T. typum* (MB.C.2118)

Faunal level 4d: Lower Domanik, 3rd Ponticeras Bed

Chut River, Outcrop 7 (BOGOSLOVSKIY 1969: Outcrop 15g, Bed 10; part of Member IVdm in KUSHNAREVA & al. 1978); sample D9213: upper MN 5 (with Ad. gigas 1, Ad. curvata early form) P. bisulcatum P. lebedeffi P. uralicum P. uchtense P. auritum P. keyserlingi (MB.C.2122.1-4) P. domanicense P. ?regale (MB.C.2123) M. ammon *T. typum* (MB.C.2119) T. contractum (MB.C.2120, Text-fig. 7C; MB.C.2742.1-2, Pl. 2, Figs. 5-6) ?Tr. keyserlingi (MB.C.2121.1-2, from conodont residue) Lb. timanicus (MB.C.2131) breviconic nautiloid (MB.C.2735)

(?) Chut River, 400 downstream from bridge, 2nd loose block (leg. RTB 1994) *P. tschernyschewi* (MB.C.2134) *P. keyserlingi* (MB.C.2135) *P. cf. bisulcatum* (MB.C.2136) *Ac.* aff. genundewa (MB.C.2137, Text-fig. 8D, Pl. 1, Fig. 3) *M. ammon* (MB.C.2138) *T. typum* (MB.C.2132) *T. contractum* (MB.C.2133.1-3)

(?) Chut River, right bank, ca. 5 km upstream from the bridge (BOGOSLOVSKIY 1969: Outcrop 15e) *P. tschernyschewi P. bisulcatum P. lebedeffi P. uralicum P. auritum P. uchtense P. keyserlingi P. domanicense* U. syrjanicus M. ammon Tornoceras sp. (det. T. simplex)

(?) Chut River, BOGOSLOVSKIY (1969): Outcrop 15v, 830 m downstream of (old) bridge *P. uchtense P. keyserlingi P. domanicense P. uralicum P. cf. bisulcatum* (leg. YATSKOV) *M. ammon* (leg. YATSKOV) *T. typum* (leg. YATSKOV)

Ukhta River, left bank, 500 m upstream of Chut River mouth (BOGOSLOVSKIY 1969: Outcrop 15zh) *P. tschernyschewi P. lebedeffi P. uchtense P. auritum P. keyserlingi P. domanicense U. syrjanicus M. ammon M. sinuosum* (PIN 1268-1590) *?Tornoceras* sp. (det. *T. simplex*)

(?) Ukhta River, right bank, 1.5 km from Gerdiol River mouth (BOGOSLOVSKIY 1969: p. 41) *P. uchtense P. auritum P. keyserlingi U. syrjanicus Tornoceras* sp. (det. *T. simplex*)

Lyaiol River, Outcrop 1351/sample 1, light grey Lower Domanik limestone *P. bisulcatum T. typum Lb. timanicus*

?faunal level 4e, either topmost Lower Domanik or lower part of Middle Domanik

Ukhta River, Outcrop 39 (BOGOSLOVSKIY Collection; differs from Menner collection which lacks ponticeratids and which clearly belongs to the Middle Domanik, MN 6) *P. uchtense P. domanicense* ?U. syrjanicus

M. lamed Gp.

Tornoceras sp. Lobobactrites sp. 5. Nordiceras timanicum Zone (UD I-G to lower I-H)

Faunal level 5a: Middle Domanik, main part

Domanik River, right bank, Outcrop 21, Beds 96-97 (YUDINA & MOSKALENKO 1994, 1997; = Outcrop 10); middle MN 6 (with *Pa. domanicensis* s.str.) *N. timanicum* (MB.C.2139, Pl. 3, Fig. 1) *M. anmon* (MB.C.2144, Pl. 3, Figs. 2-3; MB.C.2746.1) *M. lamed* (MB.C.2143.1-2, Pl. 3, Figs. 15-16; 2746.2; 2749.1-2, Pl. 3, Fig. 4) *T. typum* (MB.C.2140) *Linguatornoceras* sp. *?Tr. keyserlingi* (MB.C.2141.1-2, Pl. 2, Figs. 11-14; 2743) *PH. frechi* (MB.C.2142.1-3, Pl. 3, Figs. 5-6; 2746.3) *Ph. cf. varicatus* (MB.C.2758, Text-fig. 9E, Pl. 3, Figs. 7-8) *Lb. ?termierorum* (MB.C.2144.1-2)

Domanik River, right bank, fauna of BOGOSLOVSKIY (compare 1969: p. 41) *M. lamed M. ammon Ph. varicatus* (fragmentary)

Lyaiol River, Outcrop 1351/sample 1, dark grey Middle Domanik limestone ?N. timanicum M. ammon M. lamed T. contractum

Lyaiol River, Outcrop 1903 *M. ammon T.* vel. *L.* sp. indet.

Lyaiol River, 23 km from mouth *M. ammon M. lamed* Gp. *T.* vel *L.* sp. indet.

Faunal level 5b: Middle Domanik, upper part

Domanik River, right bank, Outcrop 21 (YUDINA & MOSKALENKO 1994, 1997; = Outcrop 10), ca. 2 m below top of Middle Domanik; (upper) MN 6 *Manticoceras* sp. (leg. YATSKOV)

Ukhta River, left bank, near Shudayag, Outcrop 503 (= Outcrop 12), 4-5 m below top Middle Domanik; (upper) MN 6 *M. ammon M. cf. lamed Ph. frechi* *T*. vel. *L*. sp. indet. *?Tr. keyserlingi Lobobactrites* sp.

Ukhta River, left bank, near Shudayag, Outcrop 503 (=Outcrop 12), 3 m below top Middle Domanik; (upper) MN 6 *M. lamed Lobobactrites* sp.

Ukhta River, left bank, near Shudayag, Outcrop 504b; (upper) MN 6 (with *Pa. domanicensis* s.str.) *N. timanicum* (MB.C.2761.1) *M. lamed M. anmon* juv. (MB.C.2761.2, 2762)

Faunal level 5c: Upper Domanik

Lyaiol River, Outcrop 1904/sample 7 = Bed 3 (Outcrop ORLOV-1); MN 9-10 (with *Pa. proversa, Pa.* cf. *luscarensis*) *N. timanicum M. ammon M. cf. ammon* juv. (MB.C.2755, rather thick, resembling *Sphaeromanticoceras*) *M. lamed* (MB.C.2754) *Manticoceras* sp. juv. (MB.C.2756.1-4) *T.* cf. *typum L.* aff. *clausum L.* sp. juv. (MB.C.2757, with ventrolateral furrows) *Lo. strangulatum* (MB.C.2753.1-3, Text-fig. 9C-D, Pl. 3, Figs. 11-12, 17) *Lb. timanicus*

Lyaiol River, Outcrop 1904, Bed 9 (Outcrop ORLOV-1); MN 9-10 *M. lamed* Gp.

Lyaiol River, Outcrop 1904/sample 19 = Bed 12 (Outcrop ORLOV-1); MN 9-10 *N. timanicum* (MB.C.2763.1, Text-fig. 8C, Pl. 3, Figs. 13-14) *Manticoceras ammon* juv. (MB.C.2763.2) *M. lamed* juv. (MB.C.2765) *Lo. strangulatum* juv. (MB.C.2766.1-3, Pl. 3, Figs. 9-10) *T. contractum* (?juv. MB.C.2764)

Ukhta River, near Shudayag, Outcrop 13 (samples 7001/7002), topmost 2 m of Upper Domanik; MN 9-10 (with *Pa. "hassi*" s.l., *Pa. "aff. proversa") M. lamed* (including anaptychi) *M. div. sp. ?Ph frechi* ?Tr. sp. (fragmentary, not *keyserlingi*)

6. Carinoceras sp. Interval Zone (upper I-H)

Faunal level 6a: topmost Upper Domanik

Outcrop 1904, carbonate concretion level at top of the Upper Domanik, specimen seen in 1996, leg. S. YATSKOV; MN 10 (with *Pa. luscarensis*, *Pa. amplificata*) *Carinoceras* sp.

Faunal level 6b: basal Syrachoy Formation

Sandstone unit (see YUDINA & MOSKALENKO 1994: opposite p. 29, unit 3) right on top of the Vetlasyan Formation *Carinoceras* sp. (large, thinly oxyconic), leg. S. YATSKOV (vide in 1996, specimen now not available)

7. Virginoceras ljaschenkoae Zone (UD I-I)

Faunal level 7a, Lyaiol Formation, Member 2, main part

Lyaiol River, Oucrop 1906, Bed 14 M. cf. solnzevi M. lamed M. carinatum M. cf. latisellatum M. cf. cordatum C. cf. menneri ?V. ljaschenkoae L. clausum L. yudinae n.sp. (MB.C.2752)

Lyaiol River, Outcrop 1906, Bed 18; lower MN 11 goniatite indet.

Lyaiol River, Outcrop 1906, Bed 19; ?lower MN 11 C. menneri M. solnzevi (MB.C.2768) M. lamed (MB.C.2767) M. cf. carinatum Au. cf. auris L. cf. clausum L. yudinae n.sp.

Lyaiol River, Outcrop 1906, Bed 46; ?lower MN 11 *T. typum*

Lyaiol River, Outcrop 1906, Bed 52; ?lower MN 11 ?C. menneri M. cf. carinatum Manticoceras sp. indet. ?L. clausum

Lyaiol River, Outcrop 1906, Bed 54; ?lower MN 11 (near level with *Pa. elegantula* and *Pa. ederi*) ?*M. cordatum*

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?M. solnzevi

Lyaiol River, Outcrop 1906, Bed 68; lower MN 11 (above first *Pa. semichatovae*) *M. carinatum* vel *latisellatum* (fragmentary) *M. cordatum ?L. clausum*

Lyaiol River, Outcrop 1906, Bed 70; lower MN 11 M. solnzevi M. carinatum vel latisellatum (fragmentary) ?L. clausum

Lyaiol River, Outcrop 1906, Bed 74; lower MN 11 ?M. solnzevi ?M. carinatum

Lyaiol River, 23 km from mouth *M. carinatum C. menneri M. cordatum* juv. ?L. clausum

Vezhavozh River, right bank, 3.2 km from mouth, Outcrop 8, Bed 3a (see YUDINA & MOSKALENKO 1994); lower MN 11 (with *Pa. semichatovae, Pa. timanensis, Po. lodinensis*) *M. latisellatum* juv. (pathological, MB.C.2733) *M. carinatum* (MB.C.2149.1-4, Pl. 4, Fig. 12; anaptychus MB.C.2745) *M. cordatum* (MB.C.2741.1-6) *M. solnzevi* (MB.C.2150.1-2) *C. menneri* (MB.C.2151.1-6, late oxyconic, Pl. 4, Figs. 11-12) *L. clausum* (MB.C.2146) *L. yudinae* n.sp. (MB.C.2147, Pl. 4, Figs. 1-2; fragmentary MB.C.2750.1-2, Pl. 4, Figs. 5-6) *Lb. timanicus* (MB.C.2740.1-2)

Vezhavozh River, right bank, 3.2 km from mouth, Outcrop 8, Bed 3h₁; lower MN 11 *M. latisellatum* (MB.C.2152.1-2) *V. ljaschenkoae* (MB.C.2153)

Vezhavozh River, right bank, 3.2 km from mouth, Outcrop 8, Bed 3q; lower MN 11 *M. solnzevi* (MB.C.2154.1-5, Pl. 4, Fig. 13) *Manticoceras* div. sp. indet. *L. clausum* (MB.C.2163)

Vezhavozh River, right bank, 3.2 km from mouth, Outcrop 8, Bed 4 (see YUDINA & MOSKALENKO 1994: p. 37 + fig.); lower MN 11 (with *Ag. triangularis*) *M. cordatum* M. cf. intumescens M. latisellatum (MB.C.2155, Pl. 4, Fig. 14) V. ljaschenkoae (MB.C.2156) T. vel. Linguat sp. (det. T. simplex)

Vezhavozh River, right bank, 3.2 km from mouth, Outcrop 8, talus slope = "Bed 5" (see Yudina & Moskalenko 1994: p. 38); lower MN 11 *M. solnzevi M. carinatum*

Vezhavozh River, Outcrop 734a; lower MN 11 (with Pa. semichatovae) M. carinatum

Vezhavozh River, Outcrop 735; lower MN 11 (with Pa. semichatovae, Pa. ederi) M. cf. cordatum C. menneri

Vezhavozh River, left bank, BOGOSLOVSKIY Outcrop I (= BOGOSLOVSKIY 1969: Outcrop 16d), 15 km from mouth at Smertel'nogo Rapids *C. menneri* (PIN 1268/30) *M.* cf. *intumescens T.* vel *L.* sp. (det. *T. simplex*)

Vezhavozh River, left bank, BOGOSLOVSKIY Outcrop II (= BOGOSLOVSKIY 1969: Outcrop 16e), 13 km from mouth *V. ljaschenkoae C. menneri* (PIN 1268/27, 1268/2130-2131) *M. solnzev* (PIN 2360, 1268/2374, 1268/2376-2378) *M. carinatum Acanthoclymenia* n.sp. juv. (MB.C.2751, Text-fig. 10A, Pl. 4, Figs. 9-10) *L. clausum* (det. *T. simplex*) (PIN 2918, 2921) *L. yudinae* n.sp. (MB.C.2760) *Lb. timanicus* (PIN 2912)

Vezhavozh River, right bank, 12.5 km from mouth BOGOSLOVSKIY Outcrop III (see BOGOSLOVSKIY 1969: p. 44) *C*. cf. *menneri* (PIN 1268/33, 1268/37-38) *M*. cf. *intumescens T*. vel. *L*. sp. (det. *T. simplex*)

Vezhavozh River, left bank, BOGOSLOVSKIY Outcrop IV (= BOGOSLOVSKIY 1969: Outcrop 16zh), 11 km from mouth, 7.5 m interval *M.* cf. *latisellatum* (PIN 2584) *M. carinatum* (PIN 2578, 2593) *M.* cf. *intumescens M. solnzevi M. cordatum* (PIN 1268/18, 1268/20)

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C. menneri

V. ljaschenkoae

[a single *M. lyaiolense*, ?from the upper part = faunal level 8, PIN 2798]]

Vezhavozh River, left bank, 7.5 km from mouth, BOGOSLOVSKIY (1969): Outcrop 16z, Bed 4 (12 cm) *M.* cf. *intumescens M. cordatum M. latisellatum V. ljaschenkoae T.* vel *L.* sp. (det. *T. simplex*)

Vezhavozh River, left bank, 7.5 km from mouth, BOGOSLOVSKIY (1969): Outcrop 16z, Bed 5 (3.5 m) *M*. cf. *intumescens*

Vezhavozh River, left bank, 7.4 km from mouth, BOGOSLOVSKIY (1969): Outcrop 16i *M. latisellatum M. cf. intumescens M. cordatum M. sinuosum* (specimen not seen !) *V. ljaschenkoae Timanoceras ellipsoidale*

Vezhavozh River, right bank, 6.5 km from mouth, BOGOSLOVSKIY (1969): Outcrop 16k, Bed 1 *M. carinatum M. solnzevi M. cf. intumescens M. cordatum T.* vel *L.* sp. (det. *T. simplex*)

Vezhavozh River, right bank, 6.5 km from mouth, BOGOSLOVSKIY (1969): Outcrop 16k, Bed 5 *M*. cf. *intumescens*

Vezhavozh River, right bank, 6.5 km from mouth, BOGOSLOVSKIY (1969): Outcrop 16k, Bed 7 *M*. cf. *intumescens*

Vezhavozh River, right bank, 6.5 km from mouth, BOGOSLOVSKIY (1969): Outcrop 16k, Bed 9 *M. carinatum M. solnzevi C. menneri V. ljaschenkoae T.* vel *L.* sp. (det. *T. simplex*)

Vezhavozh River, left bank, 6.2 km from mouth, BOGOSLOVSKIY (1969): Outcrop 161 *M*. cf. *intumescens* *M. latisellatum T.* vel *L.* sp. (det. *T. simplex*)

(?) Vezhavozh River, left bank, 5.5 km from mouth, BOGOSLOVSKIY (1969): Outcrop 16m, Bed 4 *M. cf. intumescens M. latisellatum M. carinatum M. lyaiolense* (one specimen indicating a possible younger age of this fauna, specimen not seen, possibly *M. lamed*)
(?) Vezhavozh River, left bank, 5.5 km from mouth, BOGOSLOVSKIY (1969): Outcrop 16m, Bed 6

BOGOSLOVSKIY (1969): Outcrop 16m, Bed 6 *M.* cf. *intumescens M. cordatum V. ljaschenkoae* (?the only record from higher than *M. lyaiolense*) *T.* sp. vel. *L.* sp. (det. *T. simplex*)

(?) Vezhavozh, Outcrop 7, Bed 12 V. ljaschenkoae (PIN 2502, 2531, 1268/15-16, 1268/91) *Timanoceras ellipsoidale* (PIN 1268/90, 2486) *Manticoceras* sp. indet.

Faunal level 7b: Lyaiol Formation, Member 2, upper part

Vezhavozh River, right bank, 3.2 km from mouth, Outcrop 8, Bed 6 (see Yudina & Moskalenko 1994: p. 38); upper MN 11 (with *Pa*. aff. *winchelli*) *V. ljaschenkoae*

Vezhavozh River, right bank, 3.2 km from mouth, Outcrop 8, Bed 7 (see YUDINA & MOSKALENKO 1994: p. 38); upper MN 11 (above entry of *Pa*. aff. *winchelli*) *M*. cf. *latisellatum M*. cf. *intumescens M*. cf. *lyaiolense* (not seen, record doubtful, possibly *M*. *lamed*) ?Timanoceras ellipsoidale (perhaps *M*. solnzevi)

Vezhavozh River, left bank, Outcrop 9, Bed 1; (upper) MN 11 (following correlation with upper part of Outcrop 8) ?Linguatornoceras sp. C. menneri Carinoceras div. sp. (large, compressed) V. ljaschenkoae (MB.C.2157.1-2) Manticoceras sp.

8. M. lyaiolense Zone (upper I-H to I-J)

Faunal level 8a, Lyaiol Formation, Member 2, topmost part

Vezhavozh River, left bank, 2.8 km from mouth, Outcrop 9 (YUDINA & MOSKALENKO: p. 39 + fig.), Bed 2i; upper MN 11 (with *Pa*. aff. *winchelli*) *M. latisellatum* (MB.C.2158) *M. cordatum* (MB.C.2159.1-2) *M. cf. intumescens*

Faunal level 8b, Lyaiol Formation, Member 3, basal part

Vezhavozh River, left bank, 2.8 km from mouth, Outcrop 9 (YUDINA & MOSKALENKO 1994: p. 39 + fig.), Bed 3; upper MN 11 (still with *Pa. semichatovae*, above *Pa.* aff. *winchelli*) *M. ?lamed* (det. *M.* cf. *complanatum*, not seen) *M.* cf. *cordatum*

Faunal level 8c, Lyaiol Formation, Member 3, main (middle to upper) part

Lyaiol River, Outcrop 1358, main part of Member III; ?lower MN 12 (with *Ag*. cf. *amana*, *Po*. *?imparilis*, *Pa*. *semichatovae*) *M. lamed M. cordatum M. cf. lyaiolense M. cf. latisellatum L. clausum* Vezhavozh River, left bank, 2.8 km from mouth, Outcrop 9

(YUDINA & MOSKALENKO 1994: p. 40), Bed 5; lower MN 12
(with *Pa. winchelli, foliacea*) *M.* cf. *carinatum M.* cf. *intumescens T.* vel. *L.* sp. (det. *T. simplex*)

Vezhavozh River, left bank 2.8 km from mouth, Outcrop 9 (YUDINA & MOSKALENKO 1994: p. 40), Bed 6; lower MN 12 *Manticoceras* sp.

Vezhavozh River, 2.2 km from mouth, Outcrop 10 (YUDINA & MOSKALENKO 1994: p. 40), Bed 1; MN 12 *Manticoceras* sp.

(?) Vezhavozh River, Outcrop 736a *M*. cf. *cordatum M*. cf. *lamed*

(?) enigmatic sample/specimen, allegedly from Yarega River,
3 km from mouth *Au. bickense* (elsewhere typical for latest middle Frasnian = MN 12, MB.C.2759, Text-fig. 9F, Pl. 4, Figs. 7-8)

(?) Vezhavozh River, left bank, 19.5 km from mouth,

BOGOSLOVSKIY (1969): Outcrop 16a M. carinatum M. cordatum M. cf. intumescens T. vel. L. sp. (det. T. simplex)

(?) Vezhavozh River, right bank, 18.3 km from mouth, BOGOSLOVSKIY (1969): Outcrop 16v *M. carinatum M. cf. intumescens M. cordatum T.* vel *L.* sp. (det. *T. simplex*)

(?) Vezhavozh River, right bank, 18 km from mouth, BOGOSLOVSKIY (1969): Outcrop 16b, Bed 11 (40 cm) *M. carinatum M. latisellatum M. cf. intumescens M. cordatum M. lyaiolense T.* vel. *L.* sp. (det. *T. simplex*)

(?) Vezhavozh River, right bank, 15.5 km from mouth, BOGOSLOVSKIY (1969): Outcrop 16g, Bed 4 (7-10 cm) *M. carinatum M. cf. intumescens M. latisellatum M. cordatum M. lyaiolense T.* vel. *L.* sp. (det. *T. simplex*)

(?) Vezhavozh River, right bank, 15.5 km from mouth, BOGOSLOVSKIY (1969): Outcrop 16g, Bed 8 (10 cm)*M. cordatumM. lyaiolense*

Faunal level 8d, Lyaiol Formation, Member 4, lower part

Lyaiol River, Outcrop 1359; upper MN 12 (with *Pa. gyrata*) *M. cordatum M. aff. cordatum* (intermediate to *M. intumescens*; adult

whorls not converging, thicker than *M. buchi*)) *M. lyaiolense*

Faunal level 8e, Lyaiol Formation, Member 4, middle part

Lyaiol River, Outcrop 1360 (possibly Outcrop 1359, upper part); upper MN 12 *M. lamed* (one intermediate specimen to *M. lyaiolense*) *M. cordatum*

Lyaiol River, Outcrop 1360 (V. MENNER coll.); upper MN 12

M. lamed (MB.C.2161.1-3) *M.* cf. *buchi* (MB.C.2162) *L. clausum* (MB.C.2160.1-3, Text-fig. 7F)

Lyaiol River, Outcrop 1360, sample 1; upper MN 12 (with *Ag. amana*) *M.* cf. *buchi* (more compressed than aff. *cordatum*) *M.* aff. *cordatum M.* cf. *lamed* (unusually large)

Lyaiol River, Outcrop 1360, sample 4; upper MN 12 *M*. aff. *cordatum*

Lyaiol River, Outcrop 1360, sample 5; upper MN 12 *M. cordatum M.* cf. *lamed*

Lyaiol River, Outcrop 1360, sample 7; upper MN 12 *M*. cf. *lamed* (rather large, cross-section resembling the thicker *M*. aff. *cordatum*)

Lyaiol River, Outcrop 1360, sample unspecified; upper MN 12 *M*. cf. *lamed* (with intermediates to *M*. *cordatum*) *M*. *cordatum M*. cf. *lyaiolense* (intermediate to *M*. *lamed*) *M*. *lyaiolense* (six well preserved specimens) *L*. *clausum*

Faunal level 8f, Lyaiol Formation, Member 4, upper part

Lyaiol River, Outcrop 1908, sample 1, 5-6 m below top; upper MN 12 (with *Ag. amana, Pa. orlovi, Ag.* aff. *altus, Pa.* n.sp. F) *M. lamed L. clausum*

Lyaiol River, Outcrop 1908, sample unspecified; upper MN 12 *M*. cf. *lamed*

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PLATE 1

Ammonoids from the Upper Ust'Yarega and Lower Domanik Formations

- **1-2** *Chutoceras manticoides* n.gen. n.sp. Holotype, MB.C.2165, Chut River, Outcrop 7, loose (?1st *Ponticeras* Bed), × 1
 - 1 Lateral view, showing typical sutures and concavo-convex growth ornament
 - 2 Ventral view, showing the strongly compressed cross-section with narrowly rounded venter
 - 3 Acanthoclymenia aff. genundewa (CLARKE, 1899) MB.C.2137, Chut River, loose block 400 m downstream from the bridge, probably 2nd Ponticeras Bed, × 3, lateral view of a specimen embedded in matrix which shows a typically shaped last septum
 - 4 Manticoceras sp. juv. MB.C.2701.1, Chut River, Out Crop 7, Komioceras Bed (Beds A/B), × 3, lateral view of a specimen resembling M. lamed
- **5-6** *Timanites* n.sp. MB.C.2732.1 (possible holotype), Chut River, Outcrop 7, *Komioceras* Bed (Beds A/B), × 1

5 - Lateral view, showing growth ornament without ventral lirae 6 - Ventral view

- **7-8** *Timanites keyserlingi* MILLER in MILLER & WARREN 1936 MB.C.2166, Ukhta area (outcrop unknown), *Timanites* Beds, specimen donated by D. WEYER (Magdeburg), × 1
 - 7 Lateral view, showing growth lines with distinctive ventral lirae and a thick wrinkle layer
 - 8 Ventral view

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PLATE 2

Tornoceratids from the top Ust'yarega to Middle Domanik Formations

- 1-4 Domanikoceras timidum BECKER & HOUSE, 1993 MB.C.2748, Ukhta area, probably from Chut River, Komioceras Beds (topmost Ust'yarega Formation), specimen originally deposited in the MfN as Tornoceras simplex var. ovata, adult specimen with narrow adventitious lobes, × 1.5 1 Lateral view, showing the convex growth ornament and sutures
 - 2 Ventral view showing the thickly discoidal whorl profile MB.C.2110, Chut River, Outcrop 7, Bed N (basal Domanik Formation), × 3.2
 - 3 Lateral view
 - 4 Ventral view, showing the relative broad whorls
- **5-6** *Tornoceras contractum* GLENISTER, 1958 MB.C.2742.1, Chut River, Outcrop 7, 3rd *Ponticeras* Bed, × 1.5
 - 5 Lateral view, showing the typical relative low ventral saddles of sutures
 - 6 Ventral view, showing shell compression and sutures
- **7-8** *Tornoceras typum* (SANDBERGER & SANDBERGER, 1850) MB.C.2106.1, Chut River, Outcrop 7, *Komioceras* Bed (Beds A/B), × 1.5
 - 7 Lateral view, showing sutures and subconvex growth lines
 - 8 Adoral view, showing the tegoid compressed whorl profile
- **9-10** *Linguatornoceras* aff. *clausum* (GLENISTER, 1958) MB.C.2115, Chut River, Outcrop 7, 1st *Ponticeras* Bed, × 3
 - 9 Lateral view, showing sutures
 - 10 Adoral view, showing the tegoid cross-section and last preserved septal face
- 11-14 ?*Truyolsoceras keyserlingi* (MÜLLER, 1956) MB.C.2141.2, juvenile specimen, Domanik River, Outcrop 21, Bed 97, × 6
 - 11 Ventral view, showing the strong ventrolateral furrows
 - 12 Lateral view, showing the furrows, open umbilicus, and ventral growth lirae MB.C.2141.1, early median stage, Domanik River, Outcrop 21, Bed 97, × 3
 - 13 Lateral view, showing sutures and an almost closed umbilicus.
 - 14 Ventral view, showing the compressed cross-section

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PLATE 3

Ammonoids from the Middle and Upper Domanik Formation

- 1 Nordiceras timanicum (HOLZAPFEL, 1899) MB.C.2139, Domanik River, Outcrop 21, Bed 97 (Middle Domanik Formation), × 3, lateral view of a specimen in close association with buchiolids, showing the *Ponticeras*type concavo-convex growth lines and small protoconch
- **2-3** *Manticoceras ammon* (KEYSERLING, 1844) MB.C.2144.1, Domanik River, Outcrop 21, Bed 97 (Middle Domanik Formation), × 3
 - 2 Lateral view, showing strongly biconvex growth lines at median stage
 - 3 Ventral view, showing the broadly rounded venter
 - 4 *Manticoceras lamed* (SANDBERGER & SANDBERGER, 1850) MB.C.2749.1, Domanik River, Outcrop 21, Bed 97, × 3, ventral view showing the stronger shell compression than in *M. ammon*
- **5-6** *Phoenixites frechi* (WEDEKIND, 1918) MB.C.2142.1, Domanik River, Outcrop 21, Bed 97, × 1.5

5 - Lateral view, showing parts of the last suture

6 - Ventral view, showing strong shell compression

- **7-8** *Phoenixites* cf. *varicatus* (WEDEKIND, 1918) MB.C.2758, Domanik River, Outcrop 21, Beds 96-97, × 3
 - 7 Lateral view
 - 8 Ventral view, showing shell compression and widely spaced deep constrictions
- **9-12** *Lobotornoceras strangulatum* (KEYSERLING, 1844) MB.C.2766.2, early juvenile, Lyaiol River, Outcrop 1904 (= Orlov-I), Bed 12 (sample 19), Upper Domanik Formation, × 6
 - 9 Lateral view, showing an open umbilicus and a typical convex mould constriction
 - 10 Adoral view MB.C.2753.2, juvenile, Outcrop 1904 (= Orlov-I), Bed 3 (sample 7), Upper Domanik Formation, × 6
 - 11 Lateral view, showing regularly spaced subconvex constrictions
 - 12 Ventral view, showing the typical strong shell compression
- 13-14 *Nordiceras timanicum* (HOLZAPFEL, 1899) MB.C.2763.1, Lyaiol River, Outcrop 1904 (Orlov-I), Bed 12 (sample 19), Upper Domanik Formation, × 3
 - 13 Lateral view
 - 14 Ventral view, showing extreme shell compression and ventral flattening
- **15-16** *Manticoceras lamed* (SANDBERGER & SANDBERGER, 1850) MB.C.2143.1, Domanik River, Outcrop 21, Bed 97, Middle Domanik Formation, × 4

15 - Lateral view of a small specimen

16 – Ventral view, showing the compressed whorl form

17 – *Lobotornoceras strangulatum* (KEYSERLING, 1844) MB.C.2753.1, adult specimen, Lyaiol River, Outcrop 1904 (Orlov-I), Bed 3 (sample 7), Upper Domanik Formation, × 3, lateral view, showing shell test covering a mould constriction

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PLATE 4

Ammonoids from the Lyaiol Formation, Member 2

- **1-6** *Linguatornoceras yudinae* n.sp MB.C.2147, median-sized paratype, Vezhavozh River, Outcrop 8, Bed 3a, × 2
 - 1 Lateral view, showing growth lines, the narrow ventrolateral furrow and the last septum
 - 2- Ventral view, showing an early disappearance of mould constrictions MB.C.2164, moderately large holotype, probably from Lyaiol River, $\times\,1.5$
 - 3 Lateral view, showing growth lines with narrow ventrolateral salient in a furrow and the last septum
 - 4 Ventral view with typical, densely spaced constrictions MB.C.2750.1, small specimen, Vezhavozh River, Outcrop 8, Bed 3a, × 3
 - 5 Lateral view, showing ornament and furrow
 - 6 Ventral view, showing the constrictions, bordered by spiral furrows
- **7-8** *Aulatornoceras bickense* (WEDEKIND, 1918) MB.C.2759, ?Yarega River (locality unclear), probably from the Lyaiol Formation, × 3
 - 7 Lateral view, showing the small open umbilicus and constrictions
 - 8 Ventral view, showing the broad whorls, ventral band and constrictions
- 9-10 Acanthoclymenia n.sp MB.C.2751, small specimen, Lok. 16e, × 6
 9 Lateral view, showing the last septum and small protoconch
 10 Adoral view
- 11-12 *Carinoceras menneri* LYASHENKO, 1957 MB.C.2151.1, Vezhavozh River, Outcrop 8, Bed 3a, × 1
 - 11 Ventral view
 - 12 Lateral view, showing impressed biconvex growth ornament, together with *M. carinatum* (*Beyrich*, 1837) (MB.C.2149.1)
 - **13** *Manticoceras solnzevi* LYASHENKO, 1957 MB.C.2154.4, Vezhavozh River, Outcrop 8, Bed 3q, × 2, lateral view showing a pathological interruption of septal secretion
 - 14 *Manticoceras latisellatum* JANISCHEWSKIY, 1937 MB.C.2155, Vezhavozh River, Outcrop 8, Bed 4, × 1, lateral view, showing typical wide flank saddles and a pathological flank depression

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